THE SENTINEL HYPOTHESIS:
A ROLE FOR THE MAMMALIAN SUPERIOR COLLICULUS

by

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ABSTRACT

New information on the role of the superior colliculus (SC) in spatial orientation and reactivity to sensory events was obtained in a study of the Syrian hamster. 9 animals with unilateral or bilateral lesions of the SC (some unilateral cases had forebrain control lesions contralaterally) were filmed pre- and postoperatively as they traversed a complex arena, where a wide range of controlled stimulus events triggered various forms of natural (untrained) behavioral reactions. These included approach and exploration induced by a stationary novel visual stimulus, orienting movements triggered by a transient visual distractor in a runway, fear reactions to a stationary overhead visual threat, escape responses to a moving visual threat, and finally orienting and approach to apertures baited with sunflower seeds in an open field.

Frame-by-frame analysis of motion picture records provided information on the details of the head position and orientation of the animal throughout every stimulus trial. This information on pre- and postoperative behavior was analyzed with respect to the topographic details of reconstructed collicular damage as it related to the collicular locus of representation of each of the stimulus events. The outcome of this analysis may be summarized as follows: responses in all stimulus categories showed substantial deficits after collicular lesions. According to two independent methods of data analysis, deficits were the most severe for escape to moving visual threat, followed by responses to the stationary threat, the transient visual runway distractor, and the novel visual stimulus, and were least severe for approach to apertures. Besides showing the smallest absolute deficit after collicular lesions, deficits in aperture approach were differentiated from those in other response categories by being the least clearly differentiated from the effects of forebrain control lesions, and by exhibiting substantial recovery in the course of postoperative testing. Aperture approach may therefore not be directly dependent on the SC for its successful performance, in contrast to the other response categories.

The differential severity of lesion effects across the response categories that appeared dependent on the SC for their successful performance may be interpreted as follows: the greater and more dramatic the element of escape behavior in a normal animal's response to a stimulus, the greater is the behavioral deficit produced by collicular lesions. Expressed differently, the greater the override of ongoing behavior demanded by the response to a stimulus, the more is the execution of that response dependent on the integrity of the colliculus. This interpretation of results leads to a new conception of the core functional role of the SC, expressed in the "sentinel hypothesis" which proposes that the mammalian SC is a neural mechanism that phasically overrides ongoing behavior with orienting or escape movements in response to information in the stimulus domain of distractors and threats. As such it functions as an "early warning system" designed to alert an animal and redirect its behavior in response to unexpected events outside its current focus of interest. In this capacity, part of its functional role is synonymous with the orienting reflex as classically defined, but extends beyond it to the triggering of escape behavior. This conception is explored with reference to the literature on collicular function, indicating that the sentinel hypothesis may provide a unifying conception for the behavioral role of the SC in all mammals.

Thesis Supervisor: Dr. Gerald E. Schneider
Title: Professor of Psychology and Brain Science

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Dedication

To my parents Ulla and Hellmut, who made me most of what I am; to Eugene Sachs, who taught me to think critically; and to Arthur Schopenhauer, who laid the philosophical foundations for a biology of mind.

BIOGRAPHICAL NOTE

The author was born on May 15, 1943 to a German father and a Swedish mother in the Sudetenland of World War II. His family adopted Sweden as its new homeland after arriving there as refugees at the end of the war. In high school he developed an interest in natural science, which was displaced in his late teens and early twenties by militant pacifism. This, and an interest in Eastern philosophy, led him to spend a year and a half as a volunteer with the Gandhian movement in India. From there he worked his way on ships around the world, returning to Sweden in 1966. These experiences rekindled his interest in science, particularly as it might bear on an understanding of the human mind and behavior. The step to neuroscience was short. Via an interlude as a laboratory assistant in an EEG project, and later independent studies on orienting behavior in salamanders, at The Lifwynn Foundation in Westport, Connecticut, he enrolled in the Psychology Department at Queens College of the City University of New York, where he received his B.A. in 1975. As a graduate student in the Department of Psychology and Brain Science at M.I.T. his interests and research focussed on behavioral studies of brain mechanisms controlling orienting behavior in mammals, the topic of his doctoral dissertation.

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Thanks go first to my thesis advisor, Dr. Gerald Schneider, who provided the atmosphere of intellectual freedom and disciplined curiosity which alone is capable of sustaining the spirit of scientific inquiry. His unobtrusive support and encouragement helped me pursue to completion the project reported in this thesis through hours of doubt about its feasibility. His constructive criticism at all stages of its progress has made the product a far better one than I could have delivered unaided. On behalf of my hamsters, I would also like to thank him for calming me down when I was ready to kill them for not understanding the methods section of this report. To Lucy Rava and Tony Corry, who introduced me into the mysteries of histological processing, I give thanks for being wonderful companions in the lab, and for putting up with my moods and enthusiasms. To Phil Macneil, who analyzed 664,200 frames of film, and developed tendinitis of his thumb in the effort: I could not have done it without you! Sandy Ayres I thank for her assistance in my work, and for our discussions about hamster psychology and matters farther afield. Doug Hess, David Berson, Jeremy Lanman, Tom Zeffiro, Andy Witkin, and Ed Koh I thank for being both good friends and good critics. George Sachs, Karen Hsiao, Warren Davis, Steve Wertheim, and Roberto Lent: my time in the lab would have been less interesting and fun without you! I thank Drs. David Ingle, Peter Schiller, Ann Graybiel, Alan Hein, Mel Goodale, David Milner, and Jaqueline Winterkorn for their encouragement and valuable criticism. Finally, I thank the Whitaker-Health Sciences Fund for financial support provided for my work.

"Up in the watch-tower of the head this guard looks round through the windows of the senses, and watches the point from which mischief threatens..."

Arthur Schopenhauer

INTRODUCTION

The superior colliculus (SC) is a prominent component of the mammalian midbrain, and appears to be the only site in the central nervous system where the visual, auditory, and somatosensory modalities are superposed topographically within a common efferent framework. Empirical investigation of this structure was pioneered by Flourens (1824) and Adamük (1870), relying on the ablation technique and electrical stimulation, respectively. More than a century later, despite refinements in these techniques, and the addition of physiological recording and a wealth of anatomical knowledge, there is no consensus on the basic question: What is the superior colliculus for? The quandary can be illustrated by the contrast between conceptions of collicular function derived from physiological recording and electrical stimulation of the SC, namely the "visual grasp reflex" (Hess et al., 1946) or "foveation" hypothesis, and the behavioral consequences of collicular removal in, say, the monkey.

Recording and stimulation in the monkey SC reveals an orderly topographic representation of the visual field superposed on a "motor map" such that stimulation of a given visual field position generates saccades that move the line of sight to the source of stimulation (Schiller & Koerner, 1971). This conception predicts a direct involvement of the SC in the generation of visually triggered saccades. An essentially similar arrangement is found in all mammals, provided head movements are included in the scheme for animals with limited ocular motility (Hess et al., 1946; Apter, 1946; Schaefer, 1970; Guitton et al., 1980; Roucoux et al., 1980). Mays & Sparks

(1980) critique of the foveation hypothesis, based on new physiological findings, does not argue against collicular involvement in visually triggered eye movements, but rather revises the conception of the functional organization of that involvement.

Despite the elegant simplicity of the foveation hypothesis, quantitative assessment of visually triggered eye movements in monkeys after collicular lesions discloses but minimal impairment of ocular motility. Deficits are essentially confined to increases in latency (Wurtz & Golberg, 1972) and decreases in the accuracy, number, size, and velocity of saccades (Schiller et al., 1979). The animal does not lose the "visual grasp reflex" or the capacity to acquire visual targets. This has led some investigators to abandon the foveation hypothesis in favor oa an "attentional" role for the SC (Wurtz & Goldberg, 1972), which in turn was abandoned for a "readiness to respond" conception (Wurtz & Mohler, 1976).

A different solution to the dilemma is to conceive of the SC as only one of two or more central structures capable of filling - independently - a "visual grasp" or "foveation" role. In other words, the function may be redundantly represented in the CNS. The frontal eye fields of the monkey have been suggested as such a structure because stimulation of that part of cortex, in contrast to striate cortex, evokes eye movements even after the removal of the SC (Schiller, 1977). Removal of both frontal eye fields and colliculus does indeed eliminate visually triggered eye movements, but the bearing of this result on the foveation hypothesis is difficult to assess, because the deficit extends to all forms of ocular motility including eye movements generated by optokinetic and vestibular stimulation

(Schiller et al., 1979).

Turning to results obtained in a different order of mammals, similar problems encumber the interpretation of the consequences of collicular removal in rodents. Schneider's (1969) study of visually guided behavior in the hamster assigned a prominent role to the SC in stimulus localization required for orientation to visual targets. According to this conception the hamster SC plays a role in the control of head movements analogous to the "foveation" role for the eyes of the monkey outlined above. Subsequently, however, anumber of studies have reported sparing of visually guided behavior dependent on stimulus localization after tectal lesions in rodents. In particular, it has been reported that rats and hamsters with collicular damage approach apertures with normal locomotor trajectories (Goodale & Murison, 1975; Dyer et al., 1976; Mort et al., 1980), jump accurately through an open doorway from a platform (Barnes et al., 1970), and avoid the deep side of a visual cliff (Keselica & Rosïnsky, 1976). In addition, Ingle (1981) has reported sparing of orienting and approach to targets located as far as 70^{o} from the midline in adult gerbils that had undergone neonatal colliculectomy.

These examples illustrate the lack of agreement that still exists concerning the functional role of the mammalian SC. No unitary conception of its role in the neural control of behavior has emerged from the numerous studies addressing this question. It may be that drastic species differences obscure the true state of affairs, but some of the above discrepancies pertain to a single species. Furthermore, the common features of collicular organization and connectivity throughout mammals lead to an expectation of

at least a middle ground of common functional capacity across species. In lesion studies, differences in the regional extent of tissue damage, involvement of neighboring structures, and the laminar depth of damage have often been invoked to explain discrepancies in results (see, for example, Casagrande & Diamond, 1974). Numerous methodological factors also enter the picture. For example, the studies by Pasik et al. (1966) in the monkey focussed primarily on the effect of collicular lesions on ocular motility, with negligible deficits as a result. Denny-Brown (1962) concluded that collicular removal in the monkey led to profound deficits in various forms of responsiveness, without contradicting the finding of a full range of ocular motility. His conclusions were based on a much broader, clinically oriented assessment of behavior, which may have contributed to the difference in emphasis in interpreting the collicular syndrome. Similarly, Albano & Wurtz (1978) have reported a lack of normal distractibility in colliculectomized monkeys that showed minor deficits in quantitatively assessed visually triggered eye movements. This underscores the importance of broad-based assessment of behavioral capacities in lesion studies of the SC.

Beyond anatomical and methodological differences, the current lack of a comprehensive definition of the role of the mammalian SC may point to the importance of behavioral and functional distinctions that are not commonly considered in the assessment of collicular deficits. It may be that the SC participates only in certain aspects of spatial behavior, such as orienting movements to "distractors", but is dispensable for others, such as locomotor approach or avoidance of stationary targets (see Casagrande & Diamond, 1974; Goodale & Murison, 1975; Goodale et al., 1978). If so, how is

that functional domain defined? Another variable is the visual field position within which stimuli are presented. How is the evidence that orienting and approach to targets in different visual field positions is differentially affected by collicular damage (see Sprague & Miekle, 1965; Tunkl, 1980; Ingle, 1981) to be reconciled with the fact that the entire visual field is represented in the SC? Stimulus salience and its interaction with an animal's motivational state may be another variable relevant to the interpretation of collicular deficits (see Midgley & Tees, 1979). Other factors, such as reliance on spontaneous versus reinforced responses in behavioral studies, and variable recovery times in the assessment of deficits, may also be of importance in trying to define the functional role of the SC.

In view of the numerous unanswered questions concerning the mammalian SC, the present study was designed to provide new evidence on the role of the SC in the spatial behavior of the Syrian hamster. A systematic exploration of all the above-mentioned possibilities is beyond its scope, but an attempt was made to provide a broad-based assessment of spatial ability in the hamster after collicular lesions that would bear on some of these possibilities and control for the effect of others. The approach adopted differs in significant respects from the "standard lesion experiemnt". The latter essentially aims at testing a working hypothesis about the functional role of a given structure by assessing brain damaged animals on a well established behavioral test thought to require the hypothesized function for successful performance. In the current context of uncertainty regarding a delineation of the functional domain of the mammalian SC, the limitations

of such an approach argue against its adoption.

No single behavioral test is capable of providing information relevant to any but a fraction of the issues raised above. Furthermore, a deficit on a performance criterion is not usually informative with respect to why an animal might fail on a test. Instead, the details of the behavior of hamsters was recorded as they traversed a complex arena where a wide range of specific, controlled stimulus events triggered various forms of natural (untrained) behavioral reactions. The data base of the present study was obtained from a fine-grained analysis of their head trajectories (and orientations) in space and time by means of frame-by-frame analysis of continuous motion picture records of their movements throughout every stimulus trial.

The tests incorporated in the filming arena were developed de novo through a series of pilot studies, and will be described in detail in the methods section. They rely on what appear to be the natural behavioral adaptations and spontaneous response tendencies of the Syrian hamster. In the course of self-initiated foraging trips through the arena from a nest permanently attached to the arena, an experimental animal might encounter any one of 21 different stimulus events distributed over 8 stimulus categories (see Table I, and below). These events include distractors in a runway situation, such as a truly novel stationary visual stimulus and unexpected transient visual, auditory, and somatosensory stimuli used to assess orienting reactions and exploratory activity. They further include single and multiple goals in the form of apertures baited with sunflower seeds in the walls of an open field. These provide information on orienting and locomo-

tor approach to peripheral targets, as well as distraction by and choice between multiple targets. Finally, there are stationary and moving visual threats used to study fear and escape responses. The arena also includes a maze-like arrangement of plexiglass corridors used to assess turning (motor) biases.

All tests except those involving approach to apertures rely on spontaneous, unreinforced, and readily habituable orienting or escape responses. Great care was therefore taken to distribute such trials very sparsely across filming sessions. Nevertheless, it seemed desirable to have a built-in control for habituation during post-operative testing. By relying primarily on unilateral lesions, responses on the intact side provided such a control.

The pattern of deficits in the responsiveness of hamsters with collicular damge to the different stimulus conditons (only data for visual stimuli were analyzed for this report) exhibited some unexpected features. First, the most severe deficits were found in escape to visual threat, which was abolished after collicular lesions. This finding is neither predicted by nor compatible with current conceptions of collicular function in mammals (see discussion section, p. 71). Furthermore, two independent methods of data analysis disclosed that, across the spontaneous response categories, the greater the element of escape behavior that was present in a normal hamster's response to a stimulus, the greater was the behavioral deficit produced by collicular damage. Expressed

differently - the greater the override of ongoing behavior demanded by a response to a stimulus, the more was the execution of that response dependent on the integrity of the SC. This interpretation of the results leads to a new conception of the core behavioral role of the mammalian SC. It is expressed in the "sentinel hypothesis" of collicular function as follows: The mammalian SC is a neural mechanism that phasically overrides ongoing behavior with orienting or escape responses on the basis of information in the stimulus domain of distractors and threats. As such it functions as an "early warning system" designed to alert an animal and redirect its behavior in response to unexpected events outside its current focus of interest. In this capacity part of its functional role is synonymous with the orienting reflex as classically defined, but extends beyond it to the triggering of escape behavior. The SC is explicitly not viewed as a general mechanism for target acquistion according to this view.

This conception of the behavioral role of the SC is explored in the Discussion section of this dissertation with reference to the literature on collicular function in mammals. The sentinel hypothesis appears capable of integrating a number of structural and functional properties of the SC into a common behavioral role, and may therefore provide a unifying conception of the basic behavioral role of the SC in all mammals.

METHODS

1. Experimental animals:

Nine adult, male Syrian hamsters (Mesocricetus auratus) were used in the present study. Their weights ranged from 110g to 180g.

2. Housing:

In nature, hamsters live in underground burrows and forage above ground. Experimental animals were therefore housed, 5 at a time, in a complex of individual nests permanently situated below the floor level of the testing arena (Fig. 1). The nest complex was constructed by dividing a plexiglass cylinder (66cm diameter, 15cm height) into 5 wedge-shaped compartments, completely insulated from each other by radial partitions. The circular nest complex fits into a semicircular bay at the rear of the testing arena, as shown in figure 1. The nest cylinder can be rotated in this bay, to bring one nest after another into the position used for testing a given animal (see below).

Each nest compartment has a removable lid on the top face of the cylinder. An aperture in this lid provides an exit to the arena. A plate of frosted plexiglass is attached beneath this aperture on the inside of the lid with hinges. In its raised position it covers and closes the exit, and serves as a light diffuser for a 7 watt lightbulb contained inside a light-tight cover (LF, figure 1) over the exit aperture. In its lowered position the plate serves as an exit ramp for the animal during testing sessions. In the curved outside wall of the nest two openings equipped with one way doors serve as return entrances from the arena to the nest. With a given

nest in its testing position, these return doors (RD, figure 1) line up with the exits of a left and a right return alley sloping down towards the nest from the arena floor. The doors are designed to exclude ambient light from the nest.

The floor of each nest, which contains small holes for ventilation, was covered with wood shavings which were changed periodically. A metal spout in each compartment connects to a water vial (W, figure 1) on the outside, supplying water ad libitum. Hamsters are hoarding animals, and need no deprivation to be motivated to go on foraging trips through the arena, where they collected most of their food in the form of sunflower seeds. However, any deprivation changes their behavior to persistent attemps to escape from the arena, making testing virtually impossible. To prevent this, spontaneous hoarding was supplemented with occasional food pellets delivered to the nest.

3. Light cycle and time of testing:

When not being tested, hamsters were locked in the nest by the raised exit ramp. Each nest was individually illuminated by the shielded bulb over the exit aperture, providing 14 hours light and 10 hours darkness in the nest. Hamsters are nocturnal animals, but in nature they are active at dusk (Knoop, 1954) and in the laboratory activity measurements show that they become active about one hour before light offset (Schneider, unpublished thesis), particularly if preceded by a period of dimming. These conditions were mimicked by making the one hour before light offset the only period during which animals were allowed to enter the arena for adaptation or testing. At the beginning of such a session the light fixture was re-

moved, leaving light filtering in from the arena through the exit aperture as the only, and very dim, source of light in the nest. In order to run all five animals their light cycles had to be staggered. This was done by controlling nest illumination via a five-way cam timer.

4. Testing arena:

The testing arena (figure 2) was constructed (except where noted) from white, opaque plexiglass. It consisted of a white floor measuring 66cm x 88cm, with 25cm high vertical walls. Hamsters are "escape artists" of considerable skill. They cannot scale a smooth 25cm high plexiglass wall, but can work themselves up such a wall if another surface is within about 7cm distance. All such places in the arena therefore had to be covered with a clear plexiglass ceiling. This applies to the runway or alley, the maze, and the return alleys to the nest.

The floor level of the arena is at the level of the ceiling of the nest complex. A short, removable vestibule (V, figure 1) connects the exit of a nest in the testing position with the entrance to the arena. It contains a one-way door leading into the arena, a locking device for this door under remote experimenter control, and a microswitch connected to the door hinge. The microswitch is connected to a relay which activates an overhead cine-camera when a hamster enters the arena.

The arena is divided into three major sections, labelled A, M, and F in the arena diagram of figure 2. A designates an alley or runway, 12cm wide and 36cm long. It extends from the entrance vestibule to the maze (M), and passes between two flanking compartments containing a bilaterally sym-

metrical arrangement of stimuli. These compartments are separated from the alley by coarse wire mesh (12mm x 12mm mesh size). They prevent the hamster from entering the stimulus compartments, but provide minimal obstruction of light, sound, or airpuffs emanating from the stimulus compartments. The floor and walls of the stimulus compartments are covered with yellow foam rubber to attenuate sound reflection of auditory stimuli. A "hamster-eye view" of the alley and stimulus compartments is proved in figure 3.

Four stimulus events can be delivered from these compartments, each unilaterally left or right, or bilaterally. Three of these events, namely the visual, auditory, and somatosensory transient distractors, are triggered when the animal breaks a photobeam (P, figure 2) which crosses the alley 15cm from the alley entrance. The remaining stimulus, the truly novel visual stimulus, is activated between specific trails by remote experimenter control. This is done by raising a hinged white gauze-cloth lid that covers the face of a small loudspeaker occupying position "AUD" in figure 2. This exposes the black face of the speaker, and puts the white lid in a new position above the speaker, illustrated on the right in figure 3. The stimulus is visible as soon as the animal enters the arena, at which point it is located 45^{o} lateral to the animal's straight-ahead position, subtends 13^{o} of visual angle horizontally, and extends from eye level to 26^{o} elevation.

The transient visual distractor in the alley (VIS, figure 2) consists of a triangular plate of half-silvered mirror covering the lateral front corner of the stimulus compartment. The back side of the mirror has a black "face" painted on it (figure 3, left), behind which a high intensity light

bulb (12V tensor lamp) is located and can be triggered by breaking the photobeam. When the bulb is off, the mirror reflects part of the apparatus, and when triggered on a distraction trial the panel lights up brightly, revealing the high-contrast "face" and the corner behind the mirror for approximately 390msec. (see figure 3). When the animal's head points straight ahead at the point where the photobeam is broken the visual distractor spans from 24.5^{o} to 78^{o} lateral at floor level, with its apex located 53^{o} laterally at 37^{o} elevation.

The auditory distractor is delivered via a small loudspeaker located at "ear-level" with 80^{o} eccentricity. The sharp squeaking sound of a ground-glass stopper being turned in its bottle was recorded on a 9-inch long continuous tape loop at a speed of 3.75 inches per second. It is played back through the loudspeaker at 7.5 inches per second (to maximize high frequency content) with a stimulus duration of approximately 390msec. when the animal breaks the photobeam. Not being visible on film, this stimulus is linked to an indicator light visible to the camera, but shielded from the animal, inside an indicator box at the rear of the stimulus compartment (dotted "A" in figure 2).

The somatosensory distractor, finally, consists of an air-puff generated by a "puff machine" attached to the experimenter's control panel at the front of the arena. The top of an open container was sealed with a rubber diaphragm, and its other end connected to two tubes ending immediately behind the wire mesh in the left and right stimulus compartment ("SS", figure 2). An iron disc fixed to the center of the diaphragm held it raised under tension to an electromagnet mounted above the diaphragm. Breaking the

photobeam breaks the current to the electromagnet, which releases the iron disc plus diaphragm and instantaneously delivers a mild air-puff from the tube in the stimulus compartment. In order to deliver a unilateral stimulus, the contralateral tubing is clamped. The height of the magnet over the diaphragm was adjusted so that an air-puff would be distinctly felt by a human observer placing the dorsum of his hand in the center of the alley, opposite the mouth of the tubing. Stimulus latency is less than 50msec. because the initial components of most orienting reactions to this stimulus are visible on the same frame of film (56msec/frame) that contains the onset of the indicator light (dotted "S", figure 2) to which this stimulus is linked.

A chance observation of fear responses by hamsters to overhead high contrast stimuli led to the incorporation of such a stimulus in the arena. It consists of a circular black disc which was placed on top of the clear plexiglass ceiling of the alley before the critical trial. This stimulus is visible as soon as an animal enters the alley. At that point it subtends 7.5^{o} of visual angle at an elevation of approximately 42.5^{o} on the midline of the alley.

At its distal end the alley narrows to a 6cm wide and 5cm long passage connecting the alley with the next section of the arena, the maze designated "M" in figure 2. It consists of 5cm wide plexiglass corridors, which provide four alternate routes from the alley to the "open field" ("F") of the arena. These routes are bilaterally symmetrical, and only the two in the left half of the maze will be described here. As a hamster enters the maze from the alley he faces a black plexiglass wall, "w", where he makes, say, a left turn. He can walk around this wall by then making a right turn,

and gain access to the open field by another left turn (see arrows in figure 2). Alternatively, after the initial left turn the animal can make another left turn, ascend ramp "R", and gain access to the open field by a third left turn onto bridge "B". In its initial position this bridge ends blindly at the maze wall above the exit of the maze to the open field. As the animal steps onto the bridge, which is hinged and suspended by a rubber string, it flips down under the animal's weight, allowing the hamster to leave the maze through the same exit as in the first route. This exit is filled in with black in figure 2 for the sake of identification. The first route contains two left turns and one right turn, and is half as long as the second, which contains only left turns. An added difference is the instability of the bridge as the animal steps onto it, which appears to be slightly aversive to hamsters. Normal animals, after gaining familiarity with the arena, hardly ever choose the long route, though operated animals may do so. Frequencies of route choice can be used as an index of turning or motor bias pre- and postoperatively.

Next, the animal enters the open field ("F" in figure 2). It is enclosed by the front wall of the maze, which is painted black to prevent sight of the open field from the maze, and the three plain white outer walls of the arena. At floor level straight ahead or 80^{o} left or right is a semicircular aperture in the wall. These apertures are equidistant from the maze exit, each subtending 7.25^{o} of visual angle from that point. Each aperture is backed by a sliding plexiglass plate, half of which is matt black, the other half the same white as the wall. It also contains a hole through which sunflower seeds can be inserted onto the floor immediately

in front of the aperture. Depending on the position of the sliding plate, the aperture is therefore either invisible to the hamster, or appears in high contrast black on a white background. When black, it always has a sunflower seed in front of it. On aperture trials, these stimuli are displayed either singly (left, right, or middle) or in left + right, middle + left, or middle + right combinations. A "catch trial" or "blank" condition consists of no aperture (and no seed) being visible. The middle aperture is visible and baited with a seed on all other (non-aperture) trials as well, providing the motive for traversing the maze.

From the open field a hamster can return to his nest only via a left or right return alley, marked "ret." in figure 2. The floor of these return alleys slopes downward to the one-way doors in the outside wall of the nest.

The entire arena is visually shielded from the rest of the laboratory by a white plasticized paper cover extending upwards from the outside walls on a scaffolding. In that part of the cover which extends above the front wall of the open field is a 22cm x 17cm rectangular window covered with half-silvered mirror. This allows the experimenter to view the entire inside of the arena without being visible to the experimental animal (with the room dimly lit). Below this window is a control panel from which the experimenter controls all stimulus events, doors, and the camera (see below).

In that part of the cover that extends above the left and right walls of the open field are horizontal, rectangular openings that each admit a matt black 15cm wide board suspended horizontally by strings from the

laboratory ceiling. The boards are normally kept pulled away from their opening, but when a board is released by the experimenter its leading edge is silently propelled by pendulum motion into the arena. It advances 53cm above floor level, and 18cm short of the front wall of the arena, to a maximum intrusion of 21cm. It then swings back out and is stopped. A projection onto the arena floor of the leading edge at its maximal intrusion is provided in the left part of figure 16. The stimulus event is released as an animal approaches the middle aperture for a seed, and constitutes a very effective visual threat (see results).

The upper edge of the cover-scaffolding supports a 32 watt (cool white) circular fluorescent lamp, 28cm in diameter, situated 114cm above the geometric center of the arena floor, which it illuminates. Attached to a mount extending down from the laboratory ceiling above the lamp is a Canon 1014 "Super 8" cine camera. Its lens is 137cm above the arena floor, placed concentrically with the fluorescent lamp, which does not obstruct its field of view. The field of view of the camera covers all of the arena, and no more. The camera is activated either manually from the control panel, or, during testing sessions, automatically via a relay on the entrance door to the arena. It is turned off manually, normally at the point when a hamster has picked up a sunflower seed at the end of a trial. Camera speed was always 18 frames per second.

5. Adaptation sessions:

Within a few days of the time that an animal was installed in its nest, it was given the opportunity to enter the arena during the one hour preceding light offset. The nest cylinder was rotated to the appropriate position in the bay at the back of the arena. The lighting fixture was removed from the lid of the nest, replaced with the entrance vestibule providing a covered passage to the entrance of the alley, and the exit ramp in the nest lowered to its down position. This allowed the animal to emerge from its nest, and push through the one way door in the vestibule to enter the arena. Animals that were initially reluctant to push through the door were aided by the experimenter who opened the door remotely via a string. This practice also minimized the development of superstitious behavior in negotiating the door, which could seriously interfere with the animal's subsequent progress through the alley.

On initial exposure to the arena animals showed signs of fear and caution, increasingly replaced by exploratory activity, and eventually scent-marking, "digging", gnawing, and other signs of growing familiarity. Every time the animal emerged from the nest during these adaptation sessions the middle aperture in the open field was black and baited with a sunflower seed. The animal was given every encouragement in learning the only thing it had to learn for successful performance in the arena, namely: "there will not be another seed at the aperture until I have gone back to the nest and reentered the arena". Aids included manually holding the return doors of the nest open (by remote manipulation), as well as blocking the return back to the arena from a return alley once the animal had en-

tered the return alley. This was done by lowering a clear plexiglass flap suspended on a hinge at the return alley entrance so as to block it, again by remote control from the outside. The importance of performing these manipulations remotely lies in not exposing the animal to any form of visual motion which would interfere with easily habituable escape tendencies.

The animal was never exposed to any stimulus events (except the middle aperture) during this adaptation period. After a few days the overhead camera (without film) was activated when the animal entered the arena. Initially this was done on almost every trial, then less frequently to asymptote over a few days at approximately every third trial, which is the average frequency of "stimulus trials" in formal testing sessions (see below). Pre-testing adaptation was considered complete when an animal performed 20 to 30 so called "straight runs" in the course of a one hour session for several consecutive days, and there was no obvious difference in the pattern of these runs when the camera was on versus off. A "straight run" consists of running straight through the alley without orienting movements or detours, then swiftly negotiating the maze by a short route, finally to proceed (usually more cautiously) across the open field floor to the seed at the middle aperture. The animal may then engage in various "hamsterisms" in various parts of the arena, such as grooming, gnawing, scent-marking, etc. before returning to the nest to re-emerge for another run. No hamster ever failed to spontaneously adopt the strategy of first doing a straight run to the seed, and <u>then</u> engaging in other activities. There was a very wide range in the time it took animals to complete their pre-testing adaptation. It ranged from three days (exceptional) to approximately one

month of daily one hour sessions, with many animals requiring two to three weeks to perform reliably.

6. Testing:

Filming of stimulus trails proceeded just like pretesting trials with the camera on, except that the camera was loaded with film. Animals were always given several warm-up trials without stimulus events at the beginning of a one hour testing session. At least one of these warm-up trials was run with the camera activated, before filming of actual stimulus trials. A stimulus trial is defined as any trial during which any stimulus event except the middle aperture stimulus is present. Such trials occurred no more frequently than every third trial, and sometimes less frequently. Care was taken to distribute habituable stimuli (all stimulus events except those involving apertures) as widely as possible across filming sessions. Approximately half-way through the present set of animals a fixed pattern of stimulus delivery had been worked out, the serial order of stimulus events, reflecting an optimal interleaving of habituable with aperture events, as well as counterbalancing of left versus right events. In this sequence no habituable event is repeated sooner than on the 42nd trial (counting both stimulus trials and the more frequent non-stimulus trials) following its most recent delivery. The stimulus sequence is presented in Table II, which also includes an additional sequence for use when a full repetition of the main sequence was deemed superfluous.

7. Surgery:

Three types of lesions were inflicted on the present series of animals

under Chloropent or Nembutal-plus-Valium anesthesia, with care taken to maintain clean operating conditions. Four animals had the superficial grey substance of their superior colliculus undercut according to the method of Schneider (1969). Three of these were unilateral undercuts, and one was bilateral. Two animals received knife cuts intended to interrupt the entirety of the brachium of the SC at the tectal-pretectal border. The surgery was performed with specially fashioned micro-knives made from the edge of carbon steel razor blades. The cut was made unilaterally (right SC) under visual guidance after bilateral aspiration of a portion of posterior neocortex and hippocampus to expose the tectal-pretectal border region. Cortical and hippocampal damage contralateral to the brachium cut served as a control lesion. Three further animals received stereotaxic knife cuts of the brachium of the superior colliculus using an approach from the lateral aspect of the skull. A specially fashioned knife (different from the above) was inserted via a micromanipulator through a slit-like opening in the skull bone (no aspiration of neocortex) at a knife angle designed to separate tectum from pretectum along the entire mediolateral extent of the brachium of the SC. These animals also sustained neocortical and hippocampal damage as a consequence of the passage of the knife, but only on the cut side and differing in its regional extent and disposition from the manual brachium cuts. Two of the animals recieved unilateral cuts, one of these receiving a second, contralateral cut after completion of a full sequence of testing (animal #11, figure 8, Left side first). The third animal received a bilateral cut in a single operation.

8. Histology:

After the completion of all testing, animals were killed by an overdose of Chloropent, perfused through the heart with normal saline followed by 10% formol saline. The brain was then removed, post-fixed in 10% formol saline, allowed to sink in sucrose-formalin, embedded in albumin-gelatin, and cut serially on a freezing microtome at 30 um for histological processing. Depending on the requirements of accurate lesion reconstruction, complete series of every 5th or 10th section were stained by all or some of the following procedures: a) cresyl violet for Nissl substance, b) a silver stain for Nissl substance developed by the author, which in addition stains regions of tissue damage heavily, c) Fink-Heimer I for degenerating axons and axon terminals, d) a radically bleached modification of c for dark-field microscopy, e) a new stain for degenerating terminals and lysosomes (Gallyas, 1980), f) a highly sensitive and selective silver stain for myelin (Gallyas, 1979), and g) Loyez hematoxylin for myelin. Animals with brachium cuts had one or both eyes injected with lul of 30 or 40uCi of an equal mixture of ^{3}H-leucine and ^{3}H-proline dissolved in sterile isotonic saline 24 hours prior to death. A complete series of sections from such brains was processed autoradiographically.

Lesion extent in cases that had the SC undercut was reconstructed by orthographic projection of all regions of tissue damage onto a standard dorsal view reconstruction of the hamster SC (schneider & Jhaveri, 1974). Projection lines of this standard dorsal view and of the tissue damage reconstruction were the same, running parallel to the midsagittal plane and a plane orthogonal to the line connecting bregma to the caudal border of

the interparietal bone (brain in situ) of the hamster skull. Because the anatomical "lines of projection" in the SC (that is, lines connecting corresponding points of the collicular topography throughout its depth) do not appear to run along the reconstruction lines, but rather obliquely to them in a caudo-ventral direction, this procedure is likely to underestimate the anterior extent of collicular damage when lesions are inflicted from a caudal approach, as in undercuts. This underestimation will be the greater the deeper the knife cut is located in the anterior SC. No attempt was made to correct for this source of error in the reconstruction, which therefore is likely to provide conservative lesion estimates. An example of both a series of frontal sections and the resulting dorsal view reconstruction of an undercut case (animal # 2) is provided in figure 5.

Tissue damage in animals with the two types of knife cut of the brachium of the SC was assessed in two ways: the actual cut was reconstructed from serial sections, and the areal distribution of radioactive label transported from the eye was projected orthographically onto the standard dorsal view reconstruction of the SC. Large discrepancies between the areal extent of collicular denervation as predicted from the reconstructed cut and as observed in the distribution of label indicated that the prediction from the cut was based on faulty assumptions about the course (depth, mediolateral organization in the optic tract, etc.) of fibers entering the SC from the eye. Only the autoradiographic evidence of denervation has, therefore, been used in the definition of lesions in these cases. Label in damaged colliculi exhibited a wide range of densities, spanning from zero density above background to apparently normal innervation from the eye. No in-

formation is available on the functional consequences of partial denervation of the collicular topography. For this reason, and in order to avoid the vexing problem of setting a grain density criterion valid across animals, only areas with zero density above background were accepted as truly denervated. This, again, is likely to provide a conservative estimate of lesion extent. Because the label is concentrated in the superficial grey substance, mismatch between reconstruction lines and "lines of projection" (see above) is not likely to play any significant role in the reconstruction of damage in brachium cut cases. Dorsal view reconstructions of all lesions are presented in figures 5 through 9.

9. Film analysis:

The contents of 205 three minute "Super 8" cassettes filmed at 18 frames per second were transferred onto standard data sheets by a person blind to the identity or history of experimental animals. Films were projected frame-by-frame onto diagrams of the alley and the open field in the arena. One diagram per trial was used. On the diagram the position of the tip of the animal's nose, and the orientation of the midline of its head, was marked for every third frame (56sec/frame). When stimulus events occurred in the alley, nose position and head orientation was marked at stimulus onset, as signalled either by the visual stimulus itself, or by the indicator light for auditory and somatosensory events. For some somatosensory events, which tended to trigger extremely rapid orienting movements, head position and orientation was marked for every frame subsequent to the first frame giving evidence of stimulus onset. The type of stimulus released was marked in symbols on the diagram, as was the animal's path

through the maze. For looming stimuli in the open field, the animal's head position and orientation at the first appearance of the black board in its opening was marked, as well as at its maximum intrusion into the arena. Trials for a given stimulus type, animal, and stage of testing were them summarized. For each trial, nose position markers were connected into a "nose trajectory". Head orientation was marked on each nose trajectory at stimulus onset, and at all significant points of high curvature along the trajectory. These trajectories with their appended orientation markers were superimposed on summary diagrams for a given stimulus type, animal, etc. The summary diagrams for all visual stimulus trials to which the 9 animals of the present study were exposed served as the behavioral data base for all subsequent data analysis. Examples are provided in figure 10 through 16.

10. Data analysis:

Because the majority of lesion cases in the present study received knife cuts of the brachium of the SC, the effect of which on the essential auditory and somatosensory input and output pathways of the SC is unknown, only data for responses to visual stimulus events were used in the present data analysis.

From a map of the topographic representation of the retina in the SC (figure 4a, from Frost & Schneider, 1979) the representation of the hamster's visual world in head-centered coordinates was reconstructed on the standard dorsal view reconstruction of the SC. This was done by assuming that the normal position of the hamster's eye in the head is such that the optical axis of the eye points 60^{o} lateral to the head midline and 30^{o}

above the horizon (Schneider, unpublished observations). After transforming the retinal coordinates by these two angular displacements, a spherical map of the hamster's visual world with its origin straight ahead was plotted on the collicular surface. The result is diagrammed in figure 4b, which also contains the collicular representation of all visual stimulus events to which animals were exposed, assuming that the head was in the "straight ahead" position. Scrutiny of initial head positions at stimulus onset (see trajectories in figures 10 through 16) discloses that deviations from this assumption are generally small. The many exceptions to this rule visible in aperture approach trajectories are only apparent. Head position is marked on these trajectories for the earliest point at which an animal's head is visible on film, which is not necessarily the point at which a left or right aperture is visible to the animal (they may still be completing their turn from the maze to the open field). From the plotted initial head position animals push out to a rather constant point just beyond the maze exit (visible as "nodal points" on the trajectory summaries in figure 11), and initiate their turn from there. Head positions at that point exhibit far less deviation from "straight ahead", but were not plotted on the diagrams because the overlap of markers would obscure individual traces.

The "stimulus world" representation in figure 4b was superimposed on each of the lesion diagrams in figures 5 through 9. This allowed quantitative estimations of the extent of "lesion-stimulus" overlap for each of the stimulus categories for each individual animal. For a given stimulus condition, animals could then be compared with respect to the magniture of lesion encroachment on the relevant part of the collicular topography, or

be sorted according to a fixed criterion for inclusion in the "lesion" group for that stimulus condition. The specific uses of the lesion-stimulus overlap measure will be described in the results section and below.

Behaviroal data were treated in two different ways in order to reduce information taken from nose-movement trajectories to numerical quantities. In the first approach a crude measure of pre- and postoperative "responsiveness" was derived for each stimulus category, and used for three kinds of data analysis, namely: an assessment of habituation to each stimulus type (figure 17, top), a comparison of deficits in hamsters with collicular undercutting, forebrain control lesions, and brachium cuts with associated forebrain damage (figure 17, middle), and an assessment of postoperative recovery from deficits (figure 17, bottom). For each animal and stimulus type, trials were divided into 3 categories. Trials which, according to a set criterion (see below), contained a normal response were assigned a value of 1.0. The absence of response was assigned a value of 0, and a category of responsiveness lacking any essential elements of the normal response were assigned a value of 0.5. For each animal (and colliculus) the sum of response values per total number of pre- or postoperative trials was expressed as a "percent responsiveness" measure.

In the case of the transient visual alley distractor, the presence or absence of a head deviation in the direction of the stimulus defined responsiveness except for deviations smaller than 20^{o} which were assigned a value of 0.5. Responsiveness to the truly novel alley stimulus (uncovered loudspeaker) had to include both approach and exploration along the screen wall (the normal response) in order to be given a score of 1.0, head devia-

tions in the direction of the stimulus without exploration receiving a 0.5 value. A response to overhead stationary threat in the alley was given a score of 1.0 only if it included signs of a "dash" under the stimulus, defined by increased running speed determined by time-markers on the trajectory. Responses without this running behavior received an intermediate score. For the moving visual threat in the open field, only responses of scrambling escape received a score of 1.0, whereas orienting movements and other types of responding without escape received a score of 0.5. Finally, approach to apertures obtained a score of 1.0 only if they fell within the envelope of normal approach trajectories and did not contain any extraneous orienting movements. If they contained such movements, or fell outside the envelope of normal approach trajectories but still got the animal to the aperture without detours, that is, if approach was simply inefficient, they were assigned a value of 0.5. All approaches to other locations in the open field or circuitous detours on the way to the aperture were assigned a score of 0. Clear examples of the three categories of approach behavior are contained in figure 11, where all trajectories in set "III" of "L apert post II,III" except the one containing the orienting movement received a score of 1.0. That exception plus all trajectories in set "II" except the one reaching the middle aperture were assigned a value of 0.5, while the latter alone received a 0.

A somewhat different approach to behavioral data reduction was employed in the "correlation analysis" (see below, and under results) which put a premium on maximal quantitative differentiation of behavioral deficits across animals. For the transient visual distractor the procedure was simi-

lar to the "responsiveness" measure above, consisting of a simple count of the proportion of all trials that did not evoke an orienting movement from a given animal. Impairment in aperture approach was estimated by measuring path length from the exit of the maze to the aperture with the aid of a perimeter, and averaging these lengths. Higher averages indicate greater impairment. The truly novel visual stimulus and the stationary threat each involve only a single stimulus trial. Path length was measured for these trials, longer paths indicating greater responsiveness to the stimulus. Responses to the moving visual threat fell into three groups: complete unresponsiveness, normal full-blown escape, and an intermediate category of partial responsiveness to the stimulus. These various measures were then used to rank order animals according to the severity of their behavioral impairment for each stimulus category. Tied ranks were assigned the average rank of the ties.

As already mentioned, collicular damage was assessed with respect to each separate stimulus category through a "lesion-stimulus overlap" measure. It was derived by direct measurement on the diagrams of the dorsal view reconstruction of lesions contained in figures 5 through 9, with superimposed stimulus representations. Measurements were performed on diagrams scaled to the size of those in figures 6 through 9. In the case of the transient visual runway distractor those parts of the triangular stimulus area that protruded beyond the lesion were drawn on 1mm thick plastic sheets. These shapes were then cut out and weighed on an analytical balance, giving a numerical estimate of stimulus area protruding beyond the lesion. For left and right aperture approach, and the stationary

visual threat, the distance in millimeters from the midpoint of the stimulus to the closest border of the lesion (negative if within a lesion, positive if beyond it) was measured. For the overhead visual threat this measure was averaged for the left and right SC of a given animal, whether both colliculi were damaged or not, because this stimulus is always represented in both colliculi. For the moving visual threat and the truly novel visual stimulus, finally, the number of millimeters any part of the stimulus protruded beyond the lesion, or the smallest distance in millimeters between any part of the stimulus and the border of the lesion if within it, was measured. These various quantities are listed for each animal below the lesion reconstructions in figures 5 through 9.

The "lesion-stimulus overlap" measure was used differently in the "responsiveness" and "correlational" type of data analysis. In the former, it was used to set a criterion for the extent of lesion-stimulus overlap required in order to include a given colliculus in the "lesion group" for a given stimulus category as follows. In the case of the transient visual distractor and the truly novel visual stimulus no more than 20% of the stimulus area was permitted to protrude beyond the lesion for that colliculus to be included in the lesion group. In the case of the stationary threat at least the representation of the stimulus in one colliculus had to be completely covered by the lesion. Data for the moving visual threat was included if the lesion did not depart from the medial edge of the SC by more than 2.0 millimeters anywhere along the stimulus representation. This criterion leads to the inclusion of the left colliculus of animal #15, but excludes the right colliculus of animal #12.

The difference in total area of lesion encorachment on the stimulus representation in these two animals is greater than is visible on the surface, because the representation of the moving threat descends along the medial wall of the SC. Aperture approach data, finally, was included for a colliculus where the aperture representation fell entirely within the lesion.

In the "correlational" anaylsis, lesion-stimulus overlap measures were simply used to rank order animals according to the extent of lesion encroachment on the collicular representation of a given stimulus category. This provided a prediction for the relative severity of behavioral impairment across animals for each stimulus category. In order to assess agreement between the ranking based on lesion-stimulus overlap and the observed behavioral impairments, ranked as described above, Spearman rank order correlation coefficients were computed across colliculi for each of the stimulus categories, and the significance of each correlation was determined according to the method of Glasser & Winter (1961). Additional details on certain aspects of the data analysis will be provided in the context of results presented in the next section.

RESULTS

1. General comments on behavior in the arena:

Before the results of quantitative assessment of lesion effects are presented, some general comments on the behavior of hamsters in the arena will be given, followed by a brief description of the responses of normal animals to the various stimulus events.

The fact that all testing was performed in a single arena, at the identical point of the light-dark cycle, and without resort to deprivation schedules, assures a certain uniformity in performance across animals by eliminating several sources of variance induced by contextual and motivational factors. The animals were unconstrained, paced themselves in initiating trials, and may be presumed to have been under the impression of simply going on foraging trips through the arena during testing sessions. By the time an animal was exposed to the first stimulus event (except the middle aperture in the open field) he was thoroughly familiar with the testing apparatus, having spent up to several weeks in daily one-hour adaptation sessions identical to testing sessions except for the absence of stimulus events. The role of this familiarity in the behavioral expression of stimulus detection will be considered in the discussion section.

Despite their great familiarity with the testing apparatus, normal animals treated the three sections of the arena (alley, maze, and open field) differentially in the sense that they showed more signs of caution and apprehension in the open field than in the alley, and least of all in the maze, which they appeared to regard as a "safe haven". This differential

treatment concides with the extent to which the three sections are "enclosed". The maze consists of plexiglass tunnels or "corridors", that is, it is completely covered or enclosed. The alley has wire screen walls, and its plexiglass ceiling is 25cm above floor level, making it "partially open". The open field, finally, is the largest part of the arena, and is completely uncovered. In crossing it for sunflower seeds placed at the middle aperture, some animals exhibited considerable signs of fear, leading some of them to "creep" along the floor with flattened ears towards the aperture even after weeks of familiarity with the arena. The powerful influence of these contextual factors on responses to various stimuli will be considered in the discussion section.

2. The response of normal animals to arena stimuli:

a) Transient visual runway distractor

The typical response of a normal hamster to the transient visual runway distractor was a swift orienting movement in the direction of the stimulus, with immediate resumption of locomotion towards the maze. Only rarely would animals stop to investigate on such a trial. There is a hint in those rare trials on which normal animals failed to orient to this stimulus that an element of escape may sometimes enter the response to this stimulus category. On such trials the animal's speed after stimulus onset is at the upper extreme of the normal range of speeds in that part of the alley, measured on control trials (alley traverses without stimuli). That is, an animal may speed up at stimulus onset, without orienting, indicating a possible element of escape in his behavior.

Responsiveness to the visual distractor remained high throughout long periods of testing, as illustrated in figure 17 (top). This level of responsiveness to an unexpected visual distractor that remains identical from trial to trial was not easy to achieve. Habituation had to be prevented by very infrequent delivery, as established in pilot studies. These studies also led to rejection of several previous visual distractors, including a simple small lightbulb, alternating flashes between two small lightbulbs separated by 2cm, plastic discs bobbing on springs, a styrofoam ball popping up through the floor, and a smaller cylindrical version of the half-silvered mirror lit from the inside by a tensor lamp, with or without black stripes on the inside. It appears that the large stimulus area and high contrast contour of the distraction panel that was finally adopted (see figure 3) were essential for inducing responsiveness, though this was not established parametrically, but through trial and error.

b) Truly novel visual stimulus

The truly novel visual stimulus in the alley (uncovered loudspeaker) appears to elicit pure approach and investigative behavior. The animal approaches the screen on the side of the stimulus as soon as he enters the alley, and he then may spend considerable time sniffing, pawing, and moving back and forth along the screen, his head generally oriented towards the stimulus, before resuming locomotion towards the maze. The pattern is well illustrated in figure 12 for animal #12.

c) Overhead stationary visual threat

Responses to the overhead stationary visual threat in the alley give

evidence of considerable fear associated with stimulus detection. Animals may attempt to return to the nest as soon as they have entered the alley, an exceedingly rare behavior in any other context. Finding the door blocked, they often vacillate in a highly characteristic manner of short forwards and backwards darting movement, before breaking into a high-velocity dash underneath the stimulus to the safety of the maze. The vacillation-dash pattern is illustrated in the preoperative trial for animal #11 in figure 12. Note that this threat stimulus has physical characteristics very similar to the "truly novel" visual runway stimulus (see methods), both essentially consisting of stationary black discs of comparable size, yet they elicit drastically different behavioral responses. This finding will be considered further in the discussion section.

d) Aperture approach

Aperture approach in the open field is illustrated in figure 11, showing preoperative approaches to left and right apertures for animal #2. As already mentioned in the methods section, initial head positions plotted on these trajectories are the first visible on film, but not necessarily those at which the animal can first see the aperture. Animals are still completing their final maze turn in the maze exit, from which they run directly out to the position visible as nodal points in the overlap of trajectories just outside the maze exit. At that point, variance in head orientation is minimal, locomotion slowed of briefly interrupted by a hesitation, followed by initiation of the turn towards the aperture and speeding of locomotion. After the turn, approach trajectories are rather direct, but often have a consistent curvature which varies from animal to animal, and

even between left and right approaches for a given animal.

Throughout many hundreds of adaptation session trials, animals faced only the middle aperture on entering the open field, and proceeded straight towards it to pick up a sunflower seed. Yet the very first time they were faced with a left or right aperture trial in preoperative testing, they turned and ran straight to the eccentric aperture in a manner very similar to later such trials. That is, the hamsters appeared to generalize instantly from their experience with the middle aperture. Exceptions to this rule were exceedingly rare (the anomalous preoperative left aperture trajectory in figure 11 was not the first trial in the set, and may have been caused by an inadvertent distraction).

Preoperative aperture conflict, when two baited apertures were simultaneously visible, is illustrated in figure 14, taken from animal #15. Note the considerable vacillation preceding choices between the middle and right apertures. This pattern of vacillation will assume some importance in the interpretation of collicular deficits at a later point, and is mentioned again below.

e) Moving visual threat

Normal responses to the moving visual threat in the open field, finally, were the most dramatic of all responses. Animals escaped explosively at the soundless appearance of the black overhead board, scrambling to safety at maximal hamster speed, sometimes tumbling over themselves in the attempt. These dramatic escapes are noteworthy in view of the claim that hamsters do not show escape behavior in response to various forms of "looming" stimuli (Rosinski & Keselica, 1977). If naive hamsters are taken from their vivari-

um cage, where they have daily exposure to the sight of moving humans, it is generally not possible to induce them to escape or avoid in response to various visual stimulus manipulations. If, however, they are housed for a week in a visually shielded environment within which they have an escape route to a shielded nest (the conditions under which the present author discovered their escape behavior) they will exhibit scrambling escape to overhead movement of a dark object, provided it is not presented repetitively. In the arena of the present experiment, escape was invariably directed at either of the return alleys to the nest, or to the exit of the maze. A plot of all preoperative escape trajectories in relation to the arena and the triggering stimulus is provided in figure 16.

Notice that in figure 16, where all escapes to a left moving visual threat have been mirror-imaged across the midline, there is no invariant relationship between the side (left or right) on which the threat appeared, and the direction of escape. All escape was directed exclusively at the three exits from the open field, namely the left and right return alleys or the maze, the latter being the preferred escape route. The animal's thorough familiarity with the spatial lay-out of the arena evidently constrained escape to the only possible exits from the open field. The direction of the appearance of the threatening stimulus appears to be relegated to a secondary, and perhaps even insignificant, factor in the choice of escape direction. For example, in the four threat trials triggered by the stimulus moving in from the right (trajectories labelled "R" in figure 16), two led to escape into the left, and two into the right, return alley.

Of considerable importance for the interpretation of collicular func-

tion to follow in the Discussion is the fact that normal animals need not show the slightest indication of a head movement towards the threatening stimulus before initiating escape. This is visible on the dotted head orientation markers in figure 16, several of which show no rightward deviation compared to the initial head position at stimulus onset. Of those that do deviate to the right, most form part of an escape trajectory with a right-ward direction. Escapes were initiated either by first backing up frantically and then breaking into running escape, or by initiating the latter directly on stimulus detection. Both patterns are shown in the trajectories of animal #4 in figure 13 (escape to the left "loom" was initiated by backing up).

In addition to its immediate dramatic behavioral consequences, the moving visual threat drastically altered the behavior of normal hamsters on subsequent trials. For up to 15 minutes after such a stimulus trial animals exhibited various signs of fear, hesitancy, and caution in the arena. These after-reactions consisted of hiding in the nest for many minutes, emerging with great caution only to escape back to the nest in apparent panic on reaching the open field, staying for long periods in the maze, moving hesitantly with flattened ears and frequent cautious orienting movements, etc. These sighs of fear and apprehension waned only gradually, indicating long-lasting arousal as an after-effect of a single threat trial. No attempt was made to study these after-effects systematically, but they appear to form an important, and highly adaptive, part of the normal hamster's response to visual threat.

3. Examples of lesion effects:

Figures 10 through 15 contain examples of lesion effects selected from the data for several animals for illustrative purposes. Figures 10 and 11 contain a comparison of pre- and postoperative responses to the visual runway distractor, and aperture approach in the open field, for animal #2, a case with an extensive unilateral undercut of the SC (see figure 5). The animal ranks highly on the response deficit predicted from lesion-stimulus overlap for both the transient distractor and aperture approach. Pre- and postoperative trajectories indicate a complete absence of orienting movements to the distractor contralateral to the lesion following the undercut. Aperture approach is also drastically impaired, but in contrast to responses to the distractor, aperture approach gradually recovers. Early in the second postoperative month the approach trajectories become indistinguishable from preoperative ones. This is not the result of a learned choice stragegy ("nothing straight ahead, nothing right, so it must be left") as shown in the "catch trials" for this animal in figure 15 ("Blank"). The distribution of trajectories for these catch trials shows no consistent right or left turning; the trajectories are centered on the middle aperture with some turns in either direction.

The effect of collicular undercutting on responses to the truly novel alley stimulus (uncovered loudspeaker) is illustrated for a particularly drastic case in figure 12 (animal #12, highest predicted deficit). Contralateral to the undercut, responsiveness has been eliminated. The same figure illustrates the result of a lesion predicting one of the highest postoperative deficits in responses to the overhead stationary threat (animal

#11). The last two time markers on the pre- and postoperative trajectories are three frames (168msec) apart, illustrating the high speed of the preoperative "dash" under the stimulus. Postoperatively responsiveness has been abolished.

Postoperative responses to the moving visual threat in the open field are shown for an animal whose lesion predicts the most severe deficit (animal #17) and one with no predicted deficit (animal #4) in figure 13. Animal #4 showed "scrambling escape" to both left and right stimuli, qualitatively indistinguishable from preoperative performance, whereas animal #17 showed no trace of any response to these stimuli on either side throughout the postoperative period. Parenthetically it should be noted that if an animal escaped to the moving threat the stimulus was normally never repeated again, but if there was no evidence of any response to the stimulus it was repeated at long intervals over testing sessions to eliminate the possibility of a spurious lack of responsiveness on the initial trial. This convention accounts for the different number of trials in the two cases.

The abolition of all overt signs of stimulus detection in the moving threat situation illustrated for animal #17 in figure 13, held true for all the four animals whose collicular lesion predicted the most severe deficit in this response category. All signs of fear and apprehension normally triggered by the moving threat were also eliminated. The animals were simply unresponsive to the stimulus, and proceeded without interruption to pick up a sunflower seed at the middle aperture. Of the two animals with an intermediate predicted deficit (cases #15, right threat, and #2, left threat), one oriented to the stimulus but did not escape or show other signs of fear.

The other animal reacted with full-blown escape on a single trial. This trial was anomalous in that by mistake no aperture or seed was present in the open field. The animal therefore hesitated and vacillated upon entering the field before proceeding towards the blank middle aperture. At that point the moving threat was released, and triggered escape. There is therefore reason to believe that this animal was alerted and in a higher arousal state at stimulus onset compared to earlier and later unsuccessful attempts at eliciting escape. Of the remaining cases with low or no predicted deficit, all save one escaped the visual threat in a manner qualitatively indistinguishable from normals. Parenthetically it might be mentioned that a number of postoperative escapes were performed by animals with collicular or collicular plus forebrain damage (the collicular lesion spared the region of the topography representing the threat stimulus). They were nevertheless quite competent in guiding their extremely rapid escapes with respect to the familiar lay-out of escape routes in the arena.

Trials forcing a choice between apertures (L+R, M+L, M+R) provided a wealth of information that both supplemented data on responses to single apertures, and exhibited features that were not apparent in single aperture trials. Animal #15 received the most incomplete unilateral undercut, both in areal extent and laminar depth in the SC (figure 6). This animal had no obvious postoperative deficit in approach to single apertures as measured by path-length. In preoperative choices between double apertures (figure 14) it exhibited a distinctive bias towards choosing the left-most member of a stimulus pair. Note also the considerable vacillation, already mentioned, in the choice between a middle and right aperture. The animal

repeatedly orients from one stimulus to the other before making a choice. The incomplete right collicular undercut reversed the left choice bias to a preference for the right-most of two apertures, and eliminated conspicuous vacillation. Parenthetically, the same trend is apparent in the animal's choice of routes through the maze. Preoperatively 84% of its paths consisted of "LRL" traverses of the maze, whereas postoperatively this path was chosen on only 46% of trials.

Trajectories from animal #2 in figure 15 illustrates further the aperture conflict situation. In consonance with the motor bias induced by a right collicular undercut, the animal consistently chose the right-most member of an aperture pair. Notice, nevertheless, the conspicuous left-ward head deviation that interrupted a number of these trajectories. For example, the two left orienting movements marked by asterisks in the M+L situation measure 56 and 72 degrees of deviation from the straight ahead, respectively. Reference to the lesion reconstruction in figure 5 indicates that this extent of turning is sufficient to bring the left aperture into that portion of the SC that was spared by the undercut. No such movements occurred in a random sample of trials where a single middle aperture (figure 15, "M") was present. The leftward head deviations in the choice situation are also in a direction opposite to the right motor bias induced by the right undercut. These head movements therefore provide evidence for the availability to the animal of visual information about stimuli well within a "collicular scotoma". This information is capable of driving orienting movements, at least in the aperture situation, a finding that will be considered in the Discussion.

4. Formal data analysis:

a) Habituation

The results of formal data analysis are contained in the bar graphs of figure 17 and in Table III. The first assurance one needs in considering these results is that habituation to repetitive stimulus presentations plays no major role in comparisons of pre- and postoperative responses. Although the spontaneous response categories are highly susceptible to habituation, the timing of stimulus presentations was designed to allow full recovery of responsiveness between stimulus events. Evidence on this point was gathered by averaging responsiveness to stimuli presented on the "control" side in those 5 animals that had strictly unilateral brain damage (no collicular and no forebrain damage on one side). "Percent responsiveness" scores for stimuli presented to the intact side were averaged across animals for each stimulus category separately. The time of surgery on the contralateral side was used to divide an animal's data into "pre-" and "postoperative" periods. The effect of habituation would be to lower scores in the "postoperative" period. It should be noted that this procedure also provides a check on possible "contralateral" effects, such as release or suppression of the intact side caused by damage on the contralateral side. The outcome of this analysis is contained in the bar graphs at the top of figure 17, which do not indicate any major response decrements from pre- to postoperative sessions.

b) Lesion group comparisons

The 9 experimental animals had 3 different types of lesions. Four animals received unilateral or bilateral undercutting of the SC via a caudal

approach, which was not associated with forebrain damage. These animals provide the best estimate of the behavioral consequences of collicular damage per se, and were analyzed separately. Five animals had cuts of the brachium of the SC (BSC) associated with damage to posterior neocortex plus hippocampus. Two of these animals had a control lesion of neocortex plus hippocampus alone contralateral to the BSC lesion. Percent responsiveness to stimuli presented on the side corresponding to the forebrain control lesion was determined in these two animals for all stimulus categories. They provide an approximate control for the effect of cortical damage by itself. With the exception for these two cortical control sides, the group of BSC lesion cases (designated FB-SC in figure 17) was analyzed as an independent group.

All collicular lesions were incomplete, and in order to determine the effect of collicular damage on responsiveness to a given stimulus category, a criterion had to be set for the extent of lesion-stimulus overlap required in order to include a given colliculus in the analysis for that stimulus category. The procedure employed has been detailed in the methods section (see p. 38).

The outcome of the lesion group comparison based on the percent responsiveness measure is presented in figure 17 (middle). For each stimulus category, percent responsiveness is graphed for aggregate preoperative control trials, and postoperative trials after the three types of brain damage. These results are notable only insofar as they indicate that drastic postoperative deficits occur primarily in animals with collicular damage. Aperture approach deficits appear to be generally less severe and less clearly

differentiated from the effects of cortical control lesions than other response categories. The small number of animals and trials making up any given lesion group in this analysis induces caution in making detailed comparisons between the different bar graphs in this figure. This is an inevitable result of splitting the experimental population in to subgroups, and further selecting animals for inclusion in a given lesion group by the lesion-stimulus overlap criteria. In order to increase the data base for an at least heuristic comparison across the response categories, the percent responsiveness scores for the groups with collicular lesions in this graph (cases with collicular undercuts and brachium cuts) can simply be averaged. When this is done, responses to the moving visual threat shows the most drastic deficit (9% responsiveness), followed by the stationary threat (11%), the visual runway distractor (22%), the truly novel stimulus (36%), and finally aperture approach (49%). This rankorder of collicular deficit in responsiveness to the different stimulus categories will assume importance for the interpretation of results, and with the exception of aperture approach parallels the outcome of the correlation analysis (see below).

c) Postoperative recovery

The analysis of postoperative recovery of responses to the different stimulus categories includes animals selected by the same lesion-stimulus overlap criteria used in the lesion group comparison above, which in addition had an initial postoperative deficit (against which to assess recovery) and which were tested in the second postoperative month. The analysis compares preoperative percent responsiveness with the same measure

during two postoperative periods for all stimulus categories: responses during the first two postoperative weeks, and all responses in trials after the start of the second postoperative month. The outcome of analysis is presented in the bottom graph of figure 17. Again, aperture approach is set apart from other response categories by being the only category that shows appreciable postoperative recovery after initially more severe deficits.

d) Correlation analysis

The above analysis of collicular deficits is limited by the necessity of selecting cases according to a "lesion-stimulus overlap" measure for inclusion in the lesion group for a given stimulus category. Not only does this reduce the number of animals (or rather colliculi) on which the assessment of deficits is based, it generates differences between the sets of colliculi included in the lesion groups for different stimulus categories. It would therefore be desirable to obtain a measure of the contribution of specifically collicular damage to behavioral deficits in each stimulus category based on all damaged colliculi. The fact that all collicular lesions were incomplete, affecting different parts of the collicular topography in different animals, coupled with the exceedingly low probability that a specific pattern of topographic damage in the colliculus would be matched by the same pattern of damage to vidual topographies outside the colliculus (in animals with additional forebrain lesions), makes such an analysis feasible.

A behavior dependent on the integrity of collicular circuitry ought to show a "behavioral scotoma" in visual field positions corresponding to sub-

total collicular damage. The differential extent of lesion encroachment on the collicular representation of a given stimulus category across animals can therefore be used to rank order all damaged colliculi according to the predicted relative severity of behavioral deficit for that stimulus category. Rank ordering the observed behavioral deficit for the same colliculi then allows one to compute a rankorder correlation coefficient expressing the extent to which the topography of collicular damage is related to behavioral deficits for the stimulus category under consideration. It should be clear that such a coefficient does not measure the absolute magnitude of the behavioral deficit caused by collicular damage, but rather the topographic specificity of the collicular contribution to observed deficits. If the topographic distribution of damage to other structures is the major variable in observed deficits, then the coefficient based on collicular damage would be low, and vice versa. This correlation approach therefore ought to provide a valuable complement to the estimates of absolute deficits in responses to the different stimulus categories described above.

The procedures for computing the correlation measure have been described in the methods section. Because the analysis of postoperative recovery indicated substantial recovery of aperture approach in the postoperative period, correlation coefficients for this response category were computed for total postoperative trials as well as for the first three postoperative trials ("early" trials) and all remaining trials ("late"trials). The outcome of the correlation analysis is presented in Table III. It contains the Spearman rank order correlation coefficient along with its significance level for each of the stimulus categories. Table III discloses a wide range

of correlation coefficients across stimulus categories. It is noteworthy that the magnitude of correlation coefficients for categories of unreinforced responses (all except aperture approach) matches the rank order of the magnitudes of absolute deficits in these categories for animals with collicular damage disclosed by the responsiveness analysis above (p. 53). Concerning the correlation coefficient for the "truly novel" stimulus, which does not reach statistical significance at the 0.05 level, it should be noted that it falls just short of that level of significance by having a probability of less than 0.06 of occuring by chance. If significance of this coefficient is computed via its associated t-value, a value of 1.742 is obtained, whereas a value of 1.796 is needed for significance at the 0.05 level. Evidence for postoperative recovery of aperture approach, established by absolute deficits in the recovery data of figure 17, is present in the correlation analysis as well. If the first three postoperative trials (designated "early" in Table III) are excluded from the calculation of the correlation coefficient for aperture approach, the resulting coefficient drops below significance at the 0.05 level. This would seem to indicate that recovery starts early in postoperative testing, a fact that is also evident in the postoperative trajectories for animal #2 in figure 11.

5. The consequences of laminar differences in lesion topography:

All topographic analyses of lesions were based on the regional distribution of collicular undercutting or retinofugal deafferentation of the superficial grey substance of the SC. The superficial grey substance is, however, only one of the functionally relevant collicular laminae. Other laminae do not necessarily show the same topographic distribution of damage

as the superficial grey. This is particularly obvious in undercut cases, where the knife enters and traverses the colliculus in horizontal alignement. Because of the curvature and lateral sloping of all collicular laminae, such a cut is more likely to spare (fail to undercut) lateral regions of intermediate and deep collicular layers than medial ones. This is clearly illustrated in the frontal sections of animal #2 in figure 4. The situation is very similar for at least three of the five brachium cut cases, where the knife entered the SC horizontally from the side of the skull.

Assuming that deep collicular tissue can make a functional contribution to behavior even when its connections with the superficial grey have been severed (see Casagrande & Diamond, 1974), a greater likelihood of sparing deep collicular tissue laterally than medially would lead to false predictions of deficits when the predictions are based on reconstruction of superficial grey damage only. These false predictions would selectively pertain to responses to stimuli presented lower in the visual field, which is represented laterally in the colliculus, i.e. exactly those stimuli that fall on the lower end of the range of deficits obtained in this study.

A direct test of this possibility would have to base the entire data analysis on a reconstruction of deep collicular damage, and compare the outcome with the present results. Unfortunately, the relevant anatomical data on deep damage are not available for the five brachium cut cases, where the topography of damage had to be based on autoradiographic assessment of transported amino acids injected into the eye. Although these cases sustained deep damage, the poor correspondance between collicular deafferentation expected on the basis of a reconstruction of the knife cut and that

actually observed in autoradiographs (see methods section, p. 31) would make it even more hazardous to interpret deep collicular damage on the basis of the knife cut itself.

Fortunately, at least a rough assessment of the extent to which sparing of lateral deep collicular tissue might account for the results under consideration is available in the data at hand. Such sparing would lead to incorrect predictions in a certain direction: for stimuli lower in the visual field (lateral colliculus) there should be more cases with a higher predicted than observed deficit compared to stimuli in the upper visual field (medial colliculus). A higher predicted than observed deficit would be reflected in the correlation analysis by a numerical preponderance of negative difference scores between predicted and observed ranks across cases for a given stimulus category. A simple count of the proportion of negative difference scores in the various stimulus categories therefore provides a means for assessing the "deep sparing" explanation of the range of deficits across stimulus categories.

For the moving visual threat that proportion is 7 negative and 4 positive difference scores, for the stationary threat 2 negative and 4 positive, for the visual runway distractor 4 negative and 5 positive, for the truly novel stimulus 5 negative and 4 positive, and for aperture approach it is 5 negative and 6 positive scores. The total for upper field stimuli is therefore 9 negative and 8 positive, and for lower field stimuli 14 negative and 15 positive. This outcome lends no support to the hypothesized influence of "deep lateral" sparing on the present results. An examination of the two most extreme difference scores for each category, i.e., those scores

reflecting the largest observed departures from predictions, leads to the same conclusion: they are as likely to be negative as positive for both upper and lower field stimulus conditions. It therefore appears reasonable to conclude that "hidden sparing" of collicular tissue, i.e., a topographic distribution of damage to deeper laminae uncorrelated with the reconstructed damage to superficial grey is not likely to be a correct explanation of differential deficits across stimulus categories.

6. Summary of quantitative results:

Taken together, the above results may be summarized as follows. Responses in all stimulus categories showed the most drastic deficits in animals with collicular damage. Absolute deficits were the most severe for responses to the moving visual threat, followed by the stationary threat, visual runway distractor, and the truly novel visual distractor, and were least severe for aperture approach. Except for the latter category, the magnitude of correlation coefficients expressing the extent to which lesion-stimulus overlap in the colliculus predicted the severity of behavioral deficit across animals for each stimulus category, matched the rank order of absolute deficits in postoperative responsiveness to stimuli in these categories. Differences in the severity of deficits across stimulus categories are not likely to be explained by differences between the topography of collicular damage reconstructed with respect to the superficial grey and the pattern of damage to deeper collicular laminae. Results for deficits in aperture approach were set apart from other stimulus categories by showing the least severe absolute deficit, by being the least clearly differentiated from the effects of forebrain control lesions, and by exhibiting

substantial recovery in the course of postoperative testing.

In the discussion that follows, an attempt will be made to provide a functional interpretation of these results in terms of the place of the SC in the sensori-motor economy of hamster behavior. Implications of this interpretation for the more general problem of defining the functional role of the mammalian superior colliculus will also be explored.

DISCUSSION

1. Interpretation of results:

The results just presented must be interpreted in the context of the limitations as well as strengths of the methods adopted in the present study. Although an attempt was made to include a wide range of stimulus categories in testing brain damaged animals, no claim for an exhaustive behavioral analysis of collicular function can be made on the basis of the approach presented here. Rather, by placing the emphasis on a formal study of several types of spontaneous and unreinforced responses in the assessment of deficits, this study is complementary to most other behavioral investigations of collicular function. Its major strength consists in extending the range of behavioral tests that are sensitive to collicular damage. It will become apparent that this represents more than a trivial addition of a few more testing methods. In particular, the deficits in visually elicited escape responses demonstrated here indicate the incompleteness of "visual grasp reflex" conceptions of collicular function.

The emphasis on spontaneous response categories in this study is also a major source of its limitations. The difficulties of maintaining responsiveness of these easily habituating behaviors should not be underestimated. Long and arduous pilot studies were required in order to determine the testing conditions, stimulus characteristics, and stimulus spacing that would both elicit and maintain distraction and escape type responses sufficiently to allow data collection. Formal testing itself also became very time consuming because of the necessity for wide spacing of stimulus trials across sessions. That these efforts were nevertheless

successful is demonstrated in the habituation analysis presented in the results section and illustrated in figure 17 (top). Responsiveness to all stimulus events was maintained throughout many weeks of behavioral testing. The price paid for achieving this level of performance is simply that the aggregate data contain both fewer animals and trials than would be the case in a situation in which responsiveness is maintained through reinforcement. Given these circumstances, what light do the present results shed on the behavioral role of the SC in the hamster?

One of the more striking aspects of the data presented in figure 17 (lower two bar graphs) and in Table III, is the difference in the effect of collicular lesions on aperture approach compared to the other response categories. Not only is the absolute deficit in this behavior less severe than in other tests, but it is also less clearly differentiated from the effect of forebrain control lesions, and furthermore it is the only behavior that exhibits substantial recovery in the course of post-operative testing, even after severe initial deficits.

A genuine recovery of visually guided aperture approach is supported by the finding that animals were using visual cues as the basis for improved performance: "catch trials" where no aperture was visible rule out learned guessing strategies ("nothing straight ahead, nothing right, so it must be left") except in a single animal exposed to prolonged post-operative testing (animal #16). This implies either that spared collicular tissue has regained the capacity to direct orienting movements and approach, or that visual information from nontectal structures is being utilized to this end by the animal. The former alternative appears un-

likely in view of the lack of good evidence for recovery of responses to other categories of stimuli where impairments were produced by collicular damage (barring the hypothetical possibility of differential recovery of disparate collicular cell groups and/or pathways). This leaves the alternative, namely, that animals learn to use a different structure for guiding aperture approach after SC lesions. The plausibility of this suggestion is increased by the fact that aperture approach is set apart from all other stimulus categories in the present experiment by being the only testing condition where responses are reinforced. It is therefore conceivable that hamsters in the aperture approach situation learn to use a central structure that normally does not drive orienting and approach independently of the SC, but which through appropriate reinforcement can be made to do so. Whatever the mechanism, the rather thorough recovery of aperture approach even in cases with drastic initial deficits places this response condition in a category of its own. It does not appear to be critically dependent on the integrity of collicular circuitry for its successful performance.

In contrast to reinforced aperture approach, deficits in the spontaneous, unreinforced responses do not exhibit substantial recovery during more than a month of postoperative testing after collicular lesions. These deficits are also more drastic than those in aperture approach, and generally show a better differentiation from the deficits caused by forebrain control lesions than does aperture approach. The highest coefficients obtained in the correlation analysis also belong to the spontaneous response categories. Only the coeffiecient for responses to the truly

novel stimulus fails to reach statistical significance at the 0.05 level. The absolute deficit in responses to this stimulus is also the smallest among the spontaneous response types. It nevertheless shows no evidence of recovery postoperatively, is well differentiated from the effect of cortical control lesions, and has a correlation coefficient which although it does not reach significance at the 0.05 level comes very close (better than 0.06). It therefore conforms to the overall pattern of the other spontaneous response categories, and may provisionally be regarded as belonging with these for purposes of functional interpretation. At least by comparison with the results for aperture approach, it appears that responses to the moving and stationary visual threat, the visual runway distractor, and the "truly novel" runway stimulus are more directly dependent on the integrity of collicular circuitry for their successful performance.

Beyond this general observation, can anything more specific be said about the nature of the deficit caused by collicular damage across the spontaneous, unreinforced response categories? As pointed out in the results section, there is a striking coincidence in the rank order of behavioral deficits across the spontaneous response categories whether assessed through absolute deficits in the "responsiveness" anaylsis, or by the predictive power of the topographic details of collicular damage in the correlation approach. Both methods establish that responses to the moving visual threat in some sense are the most crucially dependent on the integrity of collicular circuitry, followed by responses to the stationary threat, the runway distractor, and finally the "truly novel" stimulus. Besides the radically different approach to data analysis represented by the

two methods, they differ in the behavioral measures on which they are based for two of the behavioral categories under consideration (stationary threat and the truly novel stimulus: see methods section). It should also be remembered that the correlation analysis includes all damaged colliculi, and reflects the relation between behavioral deficits and the topographic details of collicular damage. All of the above considerations enhance the significance of the coincidence in rank order obtained by the two methods of analysis, and encourage an attempt to solve the puzzle of what the apparently differential lesion effects across the spontaneous behavioral categories might mean.

Taking the rank order of collicular deficits across the spontaneous response categories at face value, is it related to any dimension of stimulus or response characteristics that might facilitate interpretation of the present findings? No obvious characteristics of the stimuli themselves, regarded as physical objects or events, such as their size, shape, contrast, or their being moving, stationary, transient, or sustained parallel the rankorder of deficits. There is, however, another physical stimulus characteristic that roughly predicts the rank order of deficits, namely, position in the visual field of the animal. The two stimulus conditions that yielded the highest response deficits, i.e. the two visual threats, are overhead stimuli, located high in the visual field. The other stimulus events, which exhibited lesser deficits, are located lower in the visual field, at and above eye level.

No explanation in terms of simple sparing of collicular tissue suffices to link the differential visual field position of stimulus events to

the rank order of deficits, because the topography of collicular damage in relation to the collicular locus of representation of stimulus events was taken into account in both types of data analysis. In the "responsiveness" analysis this was done by using quantitative lesion-stimulus overlap criteria for inclusion of colliculi in the "lesion group" for a given stimlus category, and in the correlation analysis the extent of lesion-stimulus overlap across animals for each stimulus category served as a quantitative measure for the ranking of colliculi according to predicted severity of behavioral deficit. The more subtle possibility that the topography of collicular damage reconstructed with respect to the superficial grey does not reflect the pattern of damage in deeper collicular laminae, and might explain the ranking of deficits, has been dealt with at some length in the results section under the heading "The consequences of laminar differences in lesion topography". In that analysis, numerical estimates of the possible role of medio-lateral differences in the extent of "hidden sparing" of deep collicular tissue provided evidence against this explanation for the ranking of deficits. Having exhausted explanations couched in terms of the topography of collicular damage, one is forced to look for functional explanations for the differential effect of collicular lesions across the spontaneous response categories.

The present results provide an interesting hint about possible functional specialization along the vertical axis (mediolaterally in the SC) of the hamster's visual field. The stationary visual threat and the truly novel alley stimulus are physically quite similar, consisting of stationary black discs visible to an animal as soon as he enters the alley, yet

they trigger radically different behavioral responses in normal animals, namely, escape and exploratory approach, respectively. It is possible that this difference might be accounted for by the fact that the stationary visual threat, because of its midline placement, is "seen" by both colliculi, and the novel distractor is not. Informal testing of hamsters with a single stimulus approaching the hamster in different visual field positions discloses that upper visual field postitions are particularly effective in eliciting escape, whereas this behavior is rare with eye-level stimulus placements (Ayres, unpublished observations), though definitive evidence on the role of the region of binocular overlap in the upper visual field is as yet lacking. Whatever the criteria that enter a hamster's definition of visual threat, it is still not clear why responses differentiated in this way should be differentially susceptible to collicular damage. Is there some facet of collicular function that makes this structure particularly curcial for responses which contain elements of escape, however defined?

The answer may be contained in a much more general correlation between response characteristics and the severity of collicular deficits in the present data: Across the spontaneous response categories, the greater and more dramatic the element of escape behavior in the normal animal's response to a stimulus, the greater is the behavioral deficit produced by collicular damage. This unexpected outcome requires more detailed commentary.

At its lower end this response dimension (defined in terms of degree of tendency to escape) is occupied by the apparently pure exploratory

approach exhibited by the normal hamster encountering the truly novel stimulus (uncovered loudspeaker) in the alley. The animal's behavior in this situation is most readily interpretable as driven by "stimulus-evoked interest". Behavioral deficits after collicular damage are the lowest whether assessed in absolute terms (36% responsiveness, see p. 53) or through correlation with lesion-stimulus overlap, which does not quite reach statistical significance at the 0.05 level.

The response to the transient visual distractor consists of a quick orienting movement, not usually followed by investigative behavior. As mentioned under results, there is some very tentative evidence that an element of escape may enter this behavioral response. It may be conceived of as driven by "cautious attentiveness". Responsiveness in animals with collicular lesions averages 22%, and the correlational measure yields a coefficient of 0.72 significant at the 0.01 level.

Responses to the stationary visual threat contain dramatic elements of escape, expressed in attempts to run back to the nest, vacillating advance-retreat, ending in a "dash" under the stimulus to the safety of the maze. This behavior is obviously driven by fear. Postoperative responsiveness is 11%, and the correlation coefficient 0.83, significant at the 0.01 level despite the fact that it is based on only 8 data pairs (each animal yields only one data pair because of the midline placement of the stimulus).

Responses to the moving visual threat, finally, are the most dramatic of all. Hamsters scramble to safety in a flurry of explosive activity which on film appears to be driven by an invisible hand, sweeping the

animal into one of the three escape routes from the open field. They sometimes fall over themselves, exposing their white belly to the camera. The behavior appears to be driven by terror. Postoperative responsiveness averages 9%, and correlational measure yields a coefficient of 0.85, significant at the 0.001 level.

The behavioral gradient from exploratory approach over cautious orienting to ever more dramatic escape (see Bindra, 1959), is paralleled by the feeling or motive gradient from interest over caution to fear and terror, and this corresponds to the rank order of dependence of these behaviors on the intactness of the colliculus, if the present results are taken at face value. A more neutral way of expressing this relationship is to say that within the behaviors under consideration, the greater the difference between an animal's ongoing behavior and the behavior normally triggered by a given stimulus event, the more devastating is collicular damage to the animal's capacity to express that behavior in response to the stimulus. Or, put another way, the greater the override of ongoing behavior demanded by a response to a stimulus, the more is the execution of that response dependent on the integrity of the colliculus. This implies a dynamic or competitive interaction between collicular function and ongoing behavior, a suggestion that will be elaborated further in the next section of the discussion.

It should be noted that the postulated interest-caution-fear, or ever-greater-tendency-to-escape gradient involves a set of behaviors that are accompanied by sign of both peripheral and central arousal. The conspicuous manifestations of fear and apprehension that were observed as

an aftereffect of moving visual threat trials in normal hamsters are indicative of the extreme arousal levels associated with responses at the upper end of the behavioral gradient. The association between various indices of arousal and behavioral reactions lower on the gradient, exemplified by orienting and alerting reactions to novel stimuli has a long history of study embodied in the literature on the orienting reflex (see Sokolov, 1963, for review). The relationship between arousal and the behavioral role of the SC will be explored in a subsequent section of the discussion.

The above interpretation of results points to a new conception of the core function of the mammalian superior colliculus. It will be defined and explored in the remainder of this discussion.

2. The sentinel hypothesis:

At the outset it must be stated that the drastic deficit in escape behavior following collicular lesions demonstrated in this study is neither predicted by nor compatible with any current conception of collicular function in mammals. The response of a normal hamster to the moving visual threat need not contain any element of turning towards the threatening stimulus whatsoever, yet the escape response is abolished by a lesion restricted to the SC. It therefore falls entirely outside the domain of "visual grasp reflex" or "foveation" models of the role of the SC. Nor is it interpretable in terms of a "readiness to respond" model, because the efficacy of eliciting an escape response on the part of the visual threat is largely predicted on the complete lack of any readiness or preparation on the part of the animal for the intrusion of the threatening stimulus into his familiar world. Deficits in escape to visual threat have been previously demonstrated in toads and frogs after tectal lesions (Ewert, 1968; Ingle, 1973) and are reported to occur in tree-shrews after deep collicular lesions (Casagrande & Diamond, 1974). Denny-Brown (1962) has also described deficits in reactions to visual threat in monkeys with collicular lesions. The demonstration of escape deficits after collicular lesions by itself forces a rethinking of the behavioral role of the mammalian SC.

In what follows, an attempt will be made to define a hypothetical "core" behavioral role for the mammalian SC by outlining the domain of afferent information on which it operates, the range of behavioral reactions it controls, and, very sketchily, the mechanism that maps the

the afferent informational domain into the efferent behavioral range.

The present results suggest that the core of collicular function is a set of unlearned, spontaneous behavioral reactions to unexpected, and therefore potentially dangerous, stimulus information. The sentinel hypothesis, in brief, proposes that the mammalian SC is a mechanism that phasically overrides ongoing behavior with orienting or escape responses on the basis of a wide range of inputs carrying information about unanticipated stimulus events. The stress on the override function of the SC is meant to imply dynamic competition between collicular and noncollicular control over behavior. The sentinel hypothesis explicitly does not view the SC as a general mechanism for target acquisition, but as a mechanism for behavioral deflection towards or away from stimuli involving whole body, head, eye and ear movements in response to a particular type of information, namely sudden, intrusive, unexpected, novel, or threatening stimulus information. In short, it operates on the stimulus domain of potential distractors and threats. As such it functions as an "early warning system" designed to alert an animal and redirect its behavior in response to unexpected events outside its current focus of interest. In this capacity, part of its functional role is synonymous with the orienting reflex as classically defined (Sokolov, 1963), but extends beyond it to the triggering of at least escape behavior. Whether the type of behavioral override represented by arrest and freezing responses falls within the output range of the SC is as yet problematical, and will be considered in the last section of this discussion.

According to the present view, the sentinel role of the SC is, in part,

the price evolution extracts from mammals for their increased capacity for purposive, goal-directed, and focussed behavior. A rodent exgaged in some absorbing task, such as intense grooming of its furry exterior, can ill afford to remain oblivious to a sudden change in its environmemt which might spell sudden death in the jaws of a predator. At the cracking of a twig, or the intrusion of a shadow into its visual periphery, grooming is instantly overridden by attentive orienting or frightened escape - provided the rodent has an intact colliculus.

Goodale et al. (1975) have reported that the slightly decreased amount of startle to intense stimuli exhibited by normal animals during periods of grooming or sniffing (purposive behaviors) compared to periods without an obvious focus of activity, is greatly exaggerated by collicular lesions. Colliculectomized animals still startle when not doing anything in particular, but show significantly depressed startle reactions while engaged in grooming or sniffing. The collicular override is missing, according to the present perspective. The more an animal's activity "closes it to the world", the more crucial is the SC for returning it to the world, should changes in it so demand. This is, in a sense, a restatement of the summary of present results given earlier in this discussion: "The greater the override of ongoing behavior demanded by a response to a stimulus, the more is the execution of that response dependent on the intergrity of the SC". Collicular and non-collicular mechanisms are in dynamic balance, and compete for control over behavior. Goal-directed, purposive behavior erects a semi-permeable barrier against distraction which the SC is specialized to break.

Like a wary sentinel charged with a narrowly defined task, the mam-

malian SC is perpetually responsive to that sudden appearance of something (it does not know what things are) that might be fatal if overlooked. When there is no intrusion, no unexpected disturbance, the SC simply maintains a vigil without participating in the guidance of behavior in any obvious way. It simply waits for the intrusion, the marginal sign of worse things to come, and when the unexpected happens it has its own sensory-motor mechanism to do the minimal to avert disaster: it drives the eyes and head to the source of the disturbance when the disturbance is small, and drives the whole animal into flight when the disturbance is large. Once gaze is on target, or escape has been triggered, the sentinel returns behavioral control to the rest of the brain, and resumes its vigil, ready for the next intrusion.

A commonplace example will serve to illustrate the role of the SC according to this perspective. If, while one is absorbed in reading a book, a cockroach happens to crawl into the periphery of one's visual field, the eyes and head "whip over" to the intruder before one quite realizes what is taking place. The reaction is immediate, reflective, and surprisingly accurate in execution. The sentinel hypothesis assigns the entire sequence of stimulus detection, override of reading, and targetting orienting movement to the SC. But as soon as the eyes rest on the cockroach, the SC withdraws from the control of behavior, forebrain mechanism analyze the intruder and guide the eyes in scrutiny, while the SC resumes its vigil, ready for another intrusion.

Whether the SC plays any role when the distracted reader returns his or her gaze to the pages of the book is less certain, however. From the

point of view of the sentinel hypothesis that depends entirely on how one conceives of the execution of the return of gaze to the book. One might imagine a "book reading" signal on hold in memory during the distraction, breaking the diversion of gaze as the novelty of the distractor wanes, and deflecting the gaze back to the book. The forbrain might very well use the SC for this return shift of gaze. A premeditated, voluntary shift of gaze back to the book would, however, be accomplished by non-collicular mechanisms according to this view.

The existence of non-collicular spatial guidance mechanisms is directly implied and required by the sentinel hypothesis. If the SC is an "override" mechanism, as outlined above, this of necessity means that there must be another (other) mechanism(s) guiding spatial behavior and orientation to stimulus information that does not override or interrupt ongoing behavior, but supports it. The paradigmatic example of such spatial orientation is an animal's ability to negotiate an obstacle course consisting of stationary objects, apertures, and passages. Evidence for the independence of this type of spatial orientation from collicular mechanisms has been obtained in tree shrews with deep collicular lesions by Casagrande & Diamond (1974), and is further supported by findings in rats and gerbils by Marshall (1978) and Goodale (1981), respectively. In nature this non-collicular spatial guidance system would be engaged in situations such as locomotion across a quiet forest floor. Here there are no sudden deflections of gaze, no precipitous escapes, but rather smooth guidance of locomotion and gaze relative to the spatial lay-out of the environment, as presently perceived and as stored in memory. The mechanism controlling this guidance is

continually updated, through the distance receptors, to take account of potential routes of travel well in advance of actually reaching them.

Subjectively we are well acquainted with the difference between the two modes of orientation in the contrast between reactions to unexpected disturbances (disrupting ongoing behavior), and our smooth negotiation of doorways, corridors, and paths where spatial information does not override or intrude on behavior, but tacitly supports it. We do not turn our gaze to the edges of doorways in order to pass through them, nor do we experience sudden increases in alerting or arousal when making turns even in unfamiliar surroundings (unless, of course, the unexpected happens, driving the sentinel into action). Anticipating a fuller discussion of the relationship between collicular function and arousal later in this discussion, the two orientation domains might be operationally distinguished by the extent to which unlearned deviations in gaze or body orientation are accompanied by signs of phasic sympathetic and EEG arousal. Reactions high on such a measure would be dependent on the midbrain tectum, whereas those low on the measure would involve the hypothesized noncollicular guidance system.

On teleological grounds, the ambient noncollicular guidance system would be expected to be concerned primarily with a wide sector of the central (frontal) behavioral space of an animal, but not with the extreme periphery. This is so because spatial information in the extreme periphery is irrelevant to the guidance of an animal's progress through a complex, stationary environment. Objects in the extreme periphery of a locomoting animal have by geometric definition already been cleared

and need not be taken into account in steering further progress. Moments before, these objects may have been within the frontal sector of space relevant to steering locomotion, but by the time they reach the visual periphery, other objects are occupying the relevant sector of space, and these are the ones whose spatial information should steer locomotion in the avoidance of obstacles and selection of paths. Parenthetically, this system might also be expected to be sensitive to visual flow patterns in performing its functions, whereas the collicular mechanism might benefit from insensitivity to such information. Some evidence in support of the latter suggestion has been reported (Schaefer, 1970).

The ambient, non-tectal orientation system may also on a priori grounds be assumed to be more intimately related to learning mechanisms than the behavioral override and alerting mechanism of the collicular system. The latter should be modifiable primarily by simple habituation to repetitive stimuli (see Horn & Hill, 1966; Cynader & Berman, 1972), whereas the former might be involved more directly in the learned acquisition of paths, locomotor habits, and general familiarity with the spatial lay-out of a complex environment. The non-tectal system may therefore be predisposed to the mediation of a range of arbitrary spatial responses to stimuli shaped by reward contingencies to a far greater extent than the collicular override system. This contrast should not be conceived of as being absolute, and may in fact apply primarily to positive reward contingencies. It would, for example, not be surprising to find that learning in fear-inducing contexts exerts a sensitizing influence on the collicular system.

The hypothesized contrast between the two orientation systems may be relevant to the interpretation of sparing of visually guided behavior in mammals with collicular lesions. A recurrent finding in studies employing response reinforcement in perimetry situations is a sparing or recovery of orienting movements to stimuli in a wide frontal sector of space, coupled with more drastic and persistent impairment in the peripheral visual field after collicular lesions (Sprague & Miekle, 1965; Tunkl, 1980; Ingle, 1981; Goodale & Milner, 1981). When animals are tested for reinforced approach to doorways or other targets in eccentric positions after collicular lesions a similar result is obtained: when targets are located within a rather wide frontal sector of space, animals appear to be unimpaired in their locomotor orientation and approach (Goodate & Murison, 1975; Winterkorn 1975; Dyer et al., 1976; Mort et al., 1980). None of these studies tested approach to targets beyong 45^{o} eccentricity. However, in a study where reinforced approach to targets located at up to 90^{o} eccentricity was tested in colliculectomized gerbils, Goodale & Purvis (1980) found that approach errors increased with increasing target eccentricity. Only extensive training enabled the animals to locate and approach the most peripheral targets. The latter finding is similar to the initial drastic deficits but eventual recovery of approach to apertures located at 80^{o} eccentricity found for hamsters with collicular lesions in the present study.

These findings create a paradon if they are interpreted only in terms of collicular function, because why should the SC with its complete visual field topography mediate certain kinds of behavior pre-

ferentially in some parts of its represented topography? A plausible alternative may be provided by invoking the hypothesized characteristics of the non-collicular guidance system. Its primary function is locomotor orientation, and intrinsic to this role is a preferential specialization for the frontal sector of space, as explained above. Complete sparing of locomotor approach to frontal eccentric targets would therefore be expected after collicular lesions, without any necessity for training or even response reinforcement. With training and response reinforcement, the non-collicular system might be brought to mediate locomotor approach beyond its optimal visual field domain, because of its proposed involvement in acquired spatial behaviors. In order to mediate spatial behaviors other than its primary locomotor guidance role, e.g. orienting movements in a perimetry task, response reinforcement may be necessary even within its optimal visual field domain. Beyond the frontal visual field, such responses would be far more difficult, but perhaps not impossible, to obtain through reward and practice.

The above interpretation has the advantage of assigning differential visual field deficits in colliculectomized animals to the behavioral role played by an independent orientation system for which a clear rationale for functional specialization within the visual field is available. In the domain of the core function of the colliculus, i.e., unreinforced spontaneous responses to distractors and threats, on the other hand, the sentinel hypothesis predicts a complete visual field deficit. Weak evidence supporting this prediction comes from deficits

in fixation of frontally placed novel stimuli obtained in colliculectomized cats by Dreher et al. (1965), replicated in kittens by Brown & Berkson (1970). The deficits in distractibility to novel peripheral stimuli and so called "glancing" behavior at much smaller eccentricities reported by Albano & Wurtz (1979) for monkeys showing negligible deficits in reinforced targetting eye movements also conform to this prediction, because, as will be discussed in the next section, "glancing" behavior may most parsiminiously be interpreted as a form of distraction. The two deficits in colliculectomized monkeys reported by these authors may therefore constitute evidence for a single deficit in distractibility throughout the visual field, as predicted by the sentinel hypothesis.

In their original study of rats with SC ablations comparing responses to novel, unreinforced distractors and reinforced locomotor approach to doorways, Goodale & Murison (1975) found a loss of orienting movements to distractors, preservation of approach to doorways. However, the behavioral response type was confounded with visual field position in this study, because distractors were placed at an eccentricity considerably exceeding that of the doorways. In a later study (Goodale et al., 1978) distractors were distributed throughout a wide range of visual field positions, with the result that distraction to unreinforced novel stimuli was spared up to approximately 50^{0} eccentricity after collicular lesions. This would seem to argue against the current proposal in that according to the sentinel hypothesis the expectation would be a full visual field deficit for orienting move-

ments and distraction to novel stimuli, but not for approach to doorways. However, in this experiment distractors were flashing lightbulbs, approach targets were lit doorways, and distraction trials were conducted in the same arena and in the same sessions used for testing approach to doorways. It is therefore possible, as pointed out by the authors, that animals may have responded to distractors on the basis of confusion between them and the lit doorways, approach to which was reinforced.

In the arena tests of the present study, distraction events were clearly separated from approach targets by being delivered in a different part of the apparatus (runway vs. open field), as well as by being physically very dissimilar (large lit panel serving as a distractor, versus a small black stimulus being the target for approach). In this situation animals with a high predicted deficit for responsiveness to the runway distractor (high lesion-stimulus overlap) failed completely to orient to this event, despite the fact that a substantial portion of the large distraction panel fell well within the approximately 50^{o} of eccentricity at issue. At floor level it spanned from approximately 25 to 80 degrees of eccentricity, with its appex located 53^{o} laterally at 37^{o} elevation (see methods section, p. 21, and figure 3). This evidence, however, is not completely decisive either, because the effective area of the stimulus panel in relation to the present issue (that portion of it falling within 50^{o} eccentricity) is smaller than the full panel to which the normal animal is exposed. It might be argued, therefore, that stimulus adequacy is confounded with visual field position

in this case. Unfortunately, decisive evidence on the question of visual field deficits to purely novel, unreinforced stimuli is not available for rodents (or any other species) at this point, but would be important to obtain in view of the present hypothesis about collicular function, and the segregation of two orientation systems.

3. The "stimulus problem": defining distractors and threats

The sentinel hypothesis, as outlined thus far, leaves numerous questions unanswered. To begin with the afferent domain, it should be obvious that for mammals the set of "distractors" and "threats" does not have a definition based on physical stimulus characteristics. The overriding variable determining the efficacy of such stimuli is the history of the animal's experience. A few repeated presentations of the moving visual threat converts it from a trigger for terrified escape to a neutral stimulus without influence over behavior. In addition to the crucial variable of novelty, which cannot be defined independently of the characteristics of the receiver (Sachs, 1967) numerous context effects constrain the responsiveness of mammals to a given stimulus type. Several such context effects were mentioned in the part of the results describing the behavior of normal animals in the arena. The differential degree of caution exhibited in the three parts of the arena appears to be a crucial determinant of responsiveness to stimuli presented in these sections of the apparatus. For example, it is quite conceivable that the normal response to the moving threat released while the animal traversed the "maze" part of the apparatus (safe haven) would be arrest and orienting towards the stimulus rather than terrified escape. Furthermore, even in the open field section of the arena, the response need not invariably be scrambling escape. If the animal were completely unfamiliar with the arena, the visual threat might very well lead to freezing rather than escape. Similar arguments can be made for all the other spontaneous response categories of the present study.

Mammals do not normally respond to isolated stimuli, but to stimulus contexts. The universe of familiar contexts exerts a powerful influence over the specifics of how a mammal will treat a given stimulus event. Anything can be a distractor, anything a threat: it depends on everything else. What a stimulus actually represents to a mammal depends crucially on its motivational state, history of experience, and the entire context of stimuli within which a given one is encountered. This "stimulus problem" has to be confronted squarely. A distractor is any novel, unfamiliar, unknown, or unanticipated event. A collicular stimulus should be thought of as one that differs from an animal's implicit definition of the composition of its current sensory field. The magnitude of the discrepancy between this definition and actual circumstances may well be the only possible measure of the extent to which a response to a given stimulus is mediated by the SC. How can one obtain such a measure, except circularly by studying the effects of collicular lesions?

The problem is an old one, and has been most directly attacked in the long line of studies on the orienting reflex (see Sokolov, 1963, for review). It should be obvious from what has been said thus far that the orienting reflex, exactly as Sokolov defines it, as least in its behavioral manifestations and stimulus requirements, falls under the sentinel hypothesis as one of the behavioral outputs of the SC (see below, section on the motor role of the SC). This is relevant to the stimulus problem in that the literature on the orienting reflex discloses close correlations between the adequacy of stimuli in triggering

the orienting reflex and a set of interconnected measures of sympathetic and central arousal. These include peripheral measures such as changes in heart rate, blood flow, the galvanic skin response, and respiration, as well as central indices reflected in the state of cortical EEG desynchrony and hippocampal theta (Sokolov, 1963, see also Elul & Marchiafava, 1964; Grastyan et al., 1959; Torii & Sugi, 1960; Sachs, 1967; Siegfried & Bureš, 1978). This association should not be taken to imply that all sources of variance in these arousal measures are relevant to the question of collicular function and the definition of the stimulus domain that triggers it into action, but simply that these indices may prove useful in arriving at a noncircular definition of collicular stimuli. It may not be a pure coincidence, for example, that there is a very close correlation between temporal fluctuations in hippocampal and collicular EEG (Routtenberg & Taub, 1973).

A non-circular definition of collicular stimuli might take the form classifying stimuli that trigger unlearned deflections of gaze and/or body orientation according to the extent to which they are accompanied by indications of phasic peripheral and central arousal. The more extreme and longlasting the arousal pattern, the more crucially dependent on the SC would the behavioral response to the stimulus be, according to this formulation. Predictions from such a classification could then be tested in behavioral experiments with colliculectomized animals.

Even if this proposal should turn out to have merit, a "stimulus problem" might still remain with respect to stimuli that generate only

moderate or negligible arousal. There is presumably a set of "marginal distractors" that will earn a casual glance or brief head turn from an animal in a relaxed and unpreoccupied state, but that would be ignored under more pressing circumstances. Their "arousal value" is, in other words, not high enough to break through the dynamic barrier of an active focus of behavioral interest, but will do so when that barrier is lowered during more leisurely circumstances. It is possible that such stimuli might be difficult to classify on the basis of central EEG criteria, though the issue merits direct investigation. In their capacity of distractors, deflecting gaze and hence overriding ongoing behavior, they nevertheless fall under the sentinel hypothesis definition of collicular stimuli.

A prominent finding in both rodents and monkeys with collicular lesions is a deficit in a type of orienting behavior variously designated as "scanning" (Mort et al., 1980), "vacillation" (this study, see Results, Fig. 18, and below), "vicarious trial and error" (Tolman, 1938, 1939; Muenzinger, 1938), and "glancing" (Albano & Wurtz, 1978). Mort et al. (1980) studied the acquisition of visual discrimination in normal hamsters and hamsters with undercut or neonatally ablated colliculi. All animals acquired competence on the discrimination task; a major difference between the two groups was a deficit in what was termed "scanning" between the two visual discriminanda in hamsters with collicular damage. "Scanning" implies an active strategy on the part of the animal, alternately orienting between the two stimulus cards in order to obtain information in the course of discrimination learning.

However, one group of "non-scanning" hamsters (neonatal lesion group) were in no way impaired in habit acquisition compared to scanning normals. The scanning behavior nevertheless seemed related to discrimination performance, because its frequency in normals increased in parallel with growing proficiency on the task.

Behavior at choice points has a long history of study under the name "vicarious trial and error", both empirically (Tolman, 1938, 1939; Muenzinger, 1938) and theoretically (Bower, 1959; Audley, 1960; Spence, 1960). In the present study, prominent vacillation was observed in many normal animals faced with pairs of apertures in the arena (M+L, M+R trials). Such behavior was drastically reduced by collicular lesions even when these were so incomplete that not even initial postoperative approach to single apertures was impaired (animal 15, Fig. 18). It should be noted that in the present experiment seed-reward did not depend on which aperture the animal chose. Every black aperture always had a sunflower seed in front of it whenever an animal approached it, and whatever the combination of apertures on a given trial happened to be. It therefore seems unlikely that so called "scanning" or "vicarious trial and error" is a behavior specifically related to visual strategies in learning situations, but rather that it should be interpreted as a response to the presence of multiple visual targets per se, that is, it represents stimulus driven distraction.

Interpreting vacillatory behavior as stimulus driven distraction makes the dependence of these behaviors on the superior colliculus directly interpretable in terms of the sentinel hypothesis. Support

for this conception also comes from recent findings on certain eye movement deficits in colliculectomized monkeys. Albano & Wurtz (1978) recorded eye movements in normal and colliculectomized monkeys spontaneously looking around a complex environment, and compared these with patterns observed in the dark. In the light, animals showed a wide range of eye movements, with smaller saccades called "glances" predominating. In the dark, the smaller saccades (less than 15°) were no longer executed, but the frequency of large saccades was the same as in the light, suggesting that the "glances" are visually elicited. Colliculectomized monkeys behaved like normals in the dark, but showed a selective reduction in the frequency of small saccades and "glances" in the light. Again, stimulus driven distraction forms the natural link between this "glancing" deficit and the sentinel hypothesis. The deficit exhibited by these same animals in responses to an irrelevant and unrewarded peripheral stimulus introduced during a visual fixation task has already been mentioned. Both types of deficit receive a common interpretation in the lack of distractibility predicted by the sentinel hypothesis. The glancing behavior deficit however, is particularly relevant to the problem of defining the lower end of the distraction range, for which it may be paradigmatic.

The covariation in normal animals of the frequency of scanning with proficiency in discrimination performance reported by Mort et al. (1980) might now receive two possible interpretations. One possibility is that as animals became more proficient at the task, stimulus discriminability increased through learning, differentiating the stimuli

into more efficient mutual distractors. It is likely that forebrain mechanisms are involved in this pattern differentiation, and their influence may be carried to the SC via the prominent corticotectal projections that originate in a great diversity of cortical regions (Sherman et al., 1979; Kawamura & Konno, 1979). Alternatively, as animals became more proficient at the task they simply started to relax (!), i.e., the competition between the task demands and marginal distractors was lessened, allowing the latter to exercise control over behavior via the collicular override system, again a good example of the lower end of the range of distractors.

It should be noted, with respect to defining the lower end of the distraction range, that deficits in pure exploratory approach, that is, approach and investigatory responses to the uncovered loudspeaker (truly novel stimulus), were found in the present study. Although the effect reached only the 0.06 level of significance in the correlation analysis, the number of trials on which this measure is based was very small. The stimulus was usually presented only once pre- and postoperatively on either side. The deficit was, however, permanent, and conforms to the sentinel hypothesis by representing a collicular deficit in stimulus-evoked distraction.

There are several reports on deficits in exploratory behavior in rodents after collicular lesions. They investigate, sniff, and rear less than normals in novel situations (Foreman et al., 1979; Marshall, 1978; Pope & Dean, 1979), and show a dramatic decrease in exploratory "head-dipping" in an open field hole board (Dean et al., 1980). Such

deficits are particularly conspicuous in that activity levels often are elevated in the very situations where exploratory deficits are observed, but within the normal range in thoroughly familiar surroundings such as the home cage (Foreman et al., 1979; see also Dean et al., 1980).

Because the deficits just described, including those of the present study, appear in novel circumstances, they should not be interpreted as global deficits in some hypothetical "spontaneous investigatory tendency", but rather as deficits in distractibility. It is the novelty of objects that drives exploratory activity. The latter wanes as stimulus novelty is converted to familiarity through habituation in the course of exploration. When initially encountered by the normal animal, a novel object diverts it from its ongoing behavior, and redirects it to exploration of the source of novelty. Deficits in these various behaviors observed after collicular lesions are therefore best interpreted as impaired distractibility, as predicted by the sentinel hypothesis. The collicular override function is missing in collicular animals, releasing them from the distraction, exploratory, and investigatory responses normally triggered by novel objects. The special case of freezing and arrest responses will be considered in the last section of this Discussion.

The empirical results on deficits in exploratory behavior after collicular lesions in rodents, along with those in vacillatory behavior at choice points, as well as "glancing" deficits in colliculectomized monkeys, are all interpretable as distractibility deficits. They provide useful information relevant to defining the lower end of the range of distractors. It is in their capacity of triggering unlearned diversions

of gaze, and not as visual objects per se, that low level distractors are collicular stimuli. If these same objects are made the targets of reinforced saccades or orienting movements, the sentinel hypothesis predicts no significant deficits after collicular lesions. The minor deficits that are observed on such tasks are most simply interpreted as the result of disconnection of extra-collicular structures from a normal collicular input, a prominent part of which consists of collicular contributions to arousal-related functions, the topic of the next section of the Discussions.

4. The role of arousal in collicular function.

A relationship between collicular function and arousal/alertness was already mentioned in the interpretation of results at the beginning of this discussion. It was also implicit throughout the discussion of novelty, context, and motivational effects above. It would seem to be a central variable in collicular function, where according to the present conception it plays a dual role. The SC serves as a major "funnel" for arousal, particularly in the modality of vision, to the brain stem reticular formation, and it receives a continuous modulatory input from that structure. To begin with the former, a role for the SC in visual arousal was first suggested by Jefferson (1958), basing this idea on the work of Pearce (1958, unpublished doctoral dissertation) on SC projections to the brain stem reticular formation (RF). Noting the absence of any direct retinal projection to the RF, he suggested the extensive collicular projections to these structures as a primary route by which the visual system efferently gains access to the so called reticular activating system and its central alerting functions. In experiments

performed by these authors, long-lasting cortical desynchrony was evoked by electrical stimulation of the SC in rabbits and cats, in a manner that depended on the depth of anesthesia. In lightly anesthetized animals collicular stimulation awakened the animal and produced up to several minutes of cortical activation, but with deeper anesthesia stimulation was without effect. This finding appears to support both a role for the SC as a source of reticular activation, and its modulation by tonic arousal levels. The suggestion that behavioral deficits after collicular removal might reflect a disconnection of the brain stem reticular formation from an essential collicular input was first made by Denny-Brown (1962). He called the SC "the primary driver of the mesencephalic reticulum".

The profound effects of anesthesia (Straschill & Hoffman, 1969; Apter, 1946; Horn & Hill, 1966) and alertness level (Sprague et al., 1968; Schaefer, 1970; Sumitomo & Hayaski, 1967) on the physiological responsiveness of the colliculus are hardly ever mentioned in models of collicular function. The fact that the characteristics of single collicular units below the superficial grey are highly dependent on alertness level, varying in responsiveness, receptive field size, movement responsiveness, and habituability depending on the state of the EEG (Sprague et al., 1968) implies that the local consequences of collicular input are gated or modulated by arousal levels. The fact that current thresholds for evoking eye movements by direct electrical stimulation of the SC are critically dependent on alertness level, rising sharply with drowsiness (see reference 84) means that collicular output is gated or modulated by arousal levels.

These effects, instead of being treated as a muisance and an impediment to clean data collection, deserve systematic study because they point directly to central arousal as a major variable in collicular function. Edwards (1980) has recently emphasized the "reticular" nature of the entirety of the SC beneath the superficial grey on cytoarchitectonic and connectionistic grounds. This perspective is entirely consonant with the present interpretation of collicular function. Those behavioral reactions normally accompanied by the most extreme arousal levels emerged with the most severe deficits after collicular lesions in the present study. Central arousal also figures prominently both in the definition of collicular responsiveness to stimuli per se, and as the variable determining what behavioral output a collicular stimulus will actually trigger (orienting reflex vs. escape, see below).

The present results permit some tentative comments on the relationship between collicular damage and arousal-related behavior. All signs of fear or arousal, so conspicuous in the normal animal's response to the moving threat, were absent, along with the overt behavioral signs of stimulus detection, in animals with a total escape deficit after collicular lesions. This implies that the colliculus itself is crucial for mediating not only the sensorimotor aspects of escape behavior, but the motivational-arousal components of such responses as well. Furthermore, these fear-arousal effects appear to have a local organization within the collicular topography. If this were not the case, one might expect collicular lesions that did not cover the representation of the threat stimulus in the colliculus nevertheless to impair the arousal-

motivational components of escape, leaving, perhaps, an orienting movement towards the threat, rather than escape from it, as the overt sign of stimulus detection. This was not the case in the present study, except in one animal whose lesion partially covered the collicular threat representation. The only other animal whose lesion predicted a partial escape deficit did not exhibit either orienting movements or escape to the threat stimulus, but on one anomalous trial (see p. 49), in which the animal was inadvertently distrubed prior to stimulus delivery, it responded with full-blown escape. This might indicate that extrinsic arousal lowers the collicular "threshold" for escape responses, i.e. an arousal signal as such, whether intrinsically generated by the SC or supplied from the outside, might be the signal that switches the SC from the orienting to the escape mode. This suggestion might be explored in part by studying the effects of low doses of amphetamine on hamster orienting and escape behavior.

In this connection it is worth emphasizing that electrical stimulation of the SC in freely moving rabbits and cats elicits orienting movements at low stimulation intensities, but full-blown escape at higher intensities (Schaefer, 1970; Syka & Radil-Weiss, 1971). There is a very rough spatial organization of escape in the rabbit colliculus, such that only anterior sites (frontal visual field) trigger backwards escape, but all points in the colliculus, including anterior ones, may trigger forward escape. The threshold for forward escape decreases towards the caudal SC. There is, in other words, only the most general biasing of escape directionality by collicular topography. This is exactly as it should be, for in escape it is not primarily the spatial location of

the threatening stimulus that should steer behavior, but rather the spatial distribution of escape routes and safe havens.

The results for escape behavior obtained in the present study are consonant with those obtained by electrical stimulation of the SC, both with respect to providing evidence for collicular mediation of such responses, and with respect to the loose topographic constraints imposed by collicular topography on their execution. The lack of a clear relationship between the side (left or right) on which the moving threat appeared, and the direction of the animal's escape, was described on p. 45 in the Results section, and is illustrated in figure 16. Normal hamsters appear to escape exclusively into the three parts of the arena which their prior familiarity has established as safe havens. Even when the escape is directed to one of the return alleys, either the right or the left route may be chosen in response to, say, a right moving threat.

The lack of a clear relationship between escape direction and the spatial location of the threatening stimulus does not appear to be the result of the constraints imposed solely by the animal's familiarity with the lay-out of the arena. In informal testing of escape behavior in hamsters conducted on a hexagonal platform without provisions for escape, animals also did not show any strong or obvious tendency to guide the direction of their escape by the locus of the threatening stimulus (Ayres, unpublished observations). These circumstances imply that the collicular topography, so important in the organization of orienting movements towards stimuli, is not used or is ineffective in the escape mode of collicular function. A hint of how such an elimination of topo-

graphic constraints might be accomplished is contained in the variation in receptive field size of collicular units below the superficial grey with the state of the EEG reported by Sprague et al. (1968). On spontaneous transitions from spindling EEG to desynchronization some of these units underwent a drastic expansion of their receptive field area, which was reversed at the appearance of EEG spindles. No units were reported to contract their receptive field with arousal. A similar phenomenon has been observed by Cynader (personal communication) while holding a unit in the intermediate grey in the course of amphetamine administration. Such a unit expanded its receptive field from a well-localized and restricted field to include the entire visual half-field subsequent to administration of the central stimulant. It is at least conceivable that the same arousal signal that was suggested to throw the switch between orienting and escape above, also is responsible for "de-constraining" collicular output from intrinsic collicular topography by drastically expanding the receptive field size of units close to the output stage.

It should be obvious that the sentinel hypothesis demands a close association between arousal/alertness and collicular functions. It proposes an involvement of the SC in behaviors spanning the range from a casual glance at a marginal distractor to terrified escape from a pouncing predator. Throughout these behaviors alertness levels, context effects, the general familiarity versus novelty of the situation, etc., determine not only the over-all responsiveness of an animal to a given stimulus, but the nature of the behavioral expression of stimulus detection as well.

Extrapolating from the evidence provided by Edwards (1980) concerning the "reticular" nature of the multimodal portion of the SC below the superficial grey, and following Denny-Brown (1962), it might be suggested that its laminar, topographic organization, size, dorsal position, and wide-spread afferentation put it in a superordinate, or regulatory, position with respect to the rest of the reticular formation as far as the phasic, "on-line", functions of that system are concerned. The more than 40 subcortical sources of afference to this collicular domain in the cat (Edwards et al., 1979), as well as the numerous projections from widespread regions of the cortex, sensory as well as nonsensory (see, e.g. Sherman et al., 1979; Kawamura & Konno, 1979), allow it to be appraised of and modulated by a great diversity of sensory and motor events, as well as motivational variables. Although the functional organization of the great majority of these inputs remains unstudied, their existence is not only compatible with the sentinel hypothesis, but is required by it. A final implication of the drastic difference in the anatomical characteristics and connections of the superficial grey substance and the rest of the underlying SC described by Edwards (1980) is that the locus of the sentinel function of the SC is to be sought below the superficial grey. This issue will receive further attention in the final section of this Discussion.

5. The motor role of the superior colliculus.

The sentinel hypothesis proposes two primary motor functions for the SC: a role in triggering escape behavior away from threats, as well as

control of the orienting reflex towards distractors. Very little can be added here concerning collicular involvement in escape behavior beyond what was said in the previous section, except that it is possible that in the mammal, as in the goldfish (Ingle, 1970), the orienting and escape functions of the SC are segregated in the descending efferent projections of the SC. In the goldfish turns towards a stimulus are abolished by cutting the crossed tectospinal pathway at the ansulate commissure, an intervention that leaves avoidance movements intact. The corresponding efferent pathway in mammals is the crossed predorsal bundle. The uncrossed descending projection in mammals takes a more lateral course through the tegmentum, opening the possibility of exploring functional differences between these distinct projections via knife-cuts and/or selective lesions of target structures (see Harting (1977) and Edwards (1980) for further anatomical details).

With respect to collicular mediation of the orienting reflex, in contrast to target acquisition generally, specified by the sentinel hypothesis, it should be noted that the orienting reflex consists of a constellation of motor adjustments that is specific to individual species, and may include eye, head, trunk, ear, and whisker movements depending on the species. The results of electrical stimulation of the SC support the sentinel hypothesis by disclosing that such stimulation does trigger the species-specific orienting reflex in all its overt behavioral manifestations, provided the experimental procedure permits expression of its various motor components (Hess et al., 1946; Schaefer, 1970; Stein & McHaffie, 1978; Stryker & Schiller, 1975; Roucoux et al., 1980; Harris,

1980; Straschill & Rieger, 1973; Syka & Radil-Weiss, 1971). The components invariably include both eye and head movements and, in animals such as the hamster, rabbit, and cat, ear and whisker movements as well (Hess et al., 1946; Schaefer, 1970; Straschill & Rieger, 1973; Syka & Radil-Weiss, 1971; Stein & McHaffie, 1978). Ear movements evoked by collicular stimulation in the rabbit are directional in a manner dependent on the locus of collicular stimulation, and are appropriate to the gaze-shift evoked from the same site (Schaefer & Schneider, 1968). The anatomical pathway for collicular control of the ear musculature has been elegantly traced by Henkel & Edwards (1978). With respect to head movements, both direct and indirect projections from the colliculus to the cervical spinal cord have been demonstrated in a variety of mammals (Altman & Carpenter, 1961; Nyberg-Hansen, 1964; Harting et al., 1973; Myers, 1963; Kuypers & Misky, 1975; Harting, 1977), giving the superior colliculus access to neck motoneurons (Anderson et al., 1971). The above argues for regarding the orienting reflex, as it is expressed in a given species, as the output of the superior colliculus, and not eye movements, head movements, or any other of its fractional components.

It has been proposed that the monkey constitutes an exception to the above generalization by having the colliculus confined to the control of eye movements only (Stryker & Schiller, 1975; Robinson & Jarvis, 1974), although its oreinting reflex consists of combined eye and head movements. It is quite conceivable that the great range of ocular motility in this species has shifted the emphasis in the motor role of the SC towards control of eye movements, but the existence of both direct and

indirect collicular projections to the cervical spinal cord in the monkey (Harting, 1977) as well as the general similarity of the descending projections to those found in other species, cautions against hasty abandonment of its role in the full orienting reflex.

Although the range of ocular motility in the monkey is rather wide, it falls far short of the full extent of its visual field which in this as in other species is represented in toto in the SC. The largest saccades evoked by collicular stimulation in the monkey have an amplitude of approximately 50^{0} (Robinson, 1972). Such saccades are evoked from the caudal-most rim of the SC which represents the extreme visual periphery, far beyond 50^{0} of retinal eccentricity. No strict "foveation" model based on eye movements alone can remain self-consistent under these empirical constraints. Acquisition of targets in the extreme visual periphery must rely on combined eye and head movements in the monkey as in other species.

In view of the above, and the demonstration that collicular stimulation in the monkey evokes both eye and head movements (Ferrier, 1876; Stryker & Shiller, 1975), what is the evidence marshalled against collicular involvement in control of head movements? There is a considerable variability in latency and threshold for stimulation evoked head movements, as well as in their size; also such movements appear to be related to the initial position of the eye in the orbit (Stryker & Schiller, 1975). These are all parameters in which evoked head movements can be contrasted with eye movements, and implicit in the interpretation of these results is the assumption that the parametric attributes of eye movements evoked

by collicular stimulation constitute the criteria by which to judge possible collicular control of head movements. This assumption surely prejudges the nature of central control of head movements, about which much less is known than about eye movements.

Indeed, positive evidence for collicular involvement in head movements is provided by the finding that the probability of evoking head movements increases with increasingly caudal stimulation sites (Stryker & Schiller, 1975). This is exactly what the visual field topography of the monkey colliculus would predict when limitations in ocular motility are taken into account. Unfortunately this interesting finding was not exploited in the study, because stimulation at all sites illustrated or discussed elicited saccades of less than 20^{o} amplitude, i.e., they were in the anterior half of the SC. Extreme deviations of the eye in the orbit were instead achieved by prolonged stimulation generating "staircases" of saccades, a highly unnatural procedure. A similar limitation is evident in the single unit study of Robinson & Jarvis (1974) in which the onset of eye movement and head movement was assessed in relation to onset of unit firing in monkeys free to move their head. Unit bursts were much better temporal predictors of the onset of eye movements than of head movements. However, recording sites were confined within the anterior $35^{\grave{o}}$ of the collicular topography, which is well within the range of monkey ocular motility. One may conclude from these studies that for regions of the collicular topography representing visual field positions within the monkey's range of ocular motility collicular function is concerned primarily with eye movements. They do not as yet permit generali-

zation of this finding to the colliculus as a whole. A full characterization of the motor role of the monkey superior colliculus, and its relation to head movement and hence the monkey orienting reflex, remains a topic for empirical investigation.

The issues involved in control of the monkey's orienting reflex become accentuated in species with even more limited ocular motility, such as the cat. Its range of ocular motility spans approximately 25^{o} from the primary position, and the cat therefore must rely on combined eye and head movements in the acquisition of more eccentric targets. Indeed, in this species all eye movements beyond a few degrees of eccentricity are accompanied by head movements (Blakemore & Donaghy, 1980; Roucoux et al., 1980). Virtually all orienting movements of the cat therefore involve an interaction of eye movements, eye position, head movement, and the vestibulo-ocular reflex (VOR). The interplay of these variables in the cat's gaze shifts is by no means fixed, whether they occur spontaneously or as a consequence of collicular stimulation (see Blakemore & Donaghy, 1980; Harris, 1980; Roucoux et al., 1980).

Gaze shifts within the cat's range of ocular motility are initiated, as in the monkey, by a saccade, followed by a head movement, and terminated by a VOR-driven counterrotation of the eyes which returns them to the primary position. In another pattern of gaze shift, towards positions beyond the oculomotor range, the head executes a sweeping turn, while the eyes repeatedly dart within their range in the same direction as the head, interrupted by ocular counterrotations predicted by a VOR gain close to one. Gaze therefore describes a "staircase", that is, a series

of partial gaze shifts punctuated by periods of fixation. In still another pattern, a large gaze shift beyond the oculomotor range is accomplished by a rapid coordinated eye and head movement in the same direction, while the VOR is suppressed to zero, and even may become negative, followed by a return of VOR gain to unity, leading to a return of the eyes close to the primary position as the head finished its movement (Roucoux et al., 1980). Gaze in this situation undergoes a rapid, large amplitude, smooth displacement to a point beyond the oculomotor range via a single eye and head movement.

In the most detailed analysis to date of collicular involvement in the cat's gaze shifting strategies, Roucoux et al. (1980) have demonstrated that the small and large unitary gaze shifts are evoked by stimulation of different parts of the collicular topography. Small gaze shifts obeying the limits of the cat's ocular motility are evoked from anterior sites, corresponding to visual field positions within the oculomotor range. Saccades are retinotopically organized, and head movements evoked from this zone are dependent on the position of the eye in the orbit. The large, unitary shifts, involving VOR suppression, are evoked from more posterior sites, corresponding to visual field positions beyond the oculomotor range. Head movements evoked from this zone are of short and rather constant latency, are not dependent on eye position, and share parametric characteristics with saccades evoked from the anterior zone, including a dependence of their amplitude and direction on the topographic site of stimulation. They may be regarded as head saccades.

Harris (1980), although in agreement with a functional subdivision

of the SC into anterior and posterior regions, elicited only eye movements within the anterior zone. Negligible or no head movements accompanied these saccades. Brief stimulation (up to 200 msec) of posterior sites elicited, primarily, combined eye and head movements with full VOR compensation, leading the gaze shift to fall short of the visual field position represented at the stimulation site. According to Harris, gaze changes beyond the oculomotor range require prolonged stimulation of posterior sites, eliciting gaze "staircases". It might be mentioned that the cats studied by Blakemore & Donaghy (1980) as well as Harris (1980) were selected for docility, whereas no such selection is mentioned by Roucoux et al. (1980). The latter authors provided a lively environment for their animals during stimulation sessions by introducing novel stimuli, morsels of favorite food, noises, and experimenter movements. No such manipulations are mentioned by Harris. Factors discussed in connection with the role of arousal in collicular function might therefore have contributed to some of the differences between the two stimulation studies.

The question arises as to how natural a mode of orienting the "gaze staircase" is. There is no doubt that cats do display this pattern of eye-head coordination (Blakemore & Donaghy, 1980), at least while spontaneously looking around a motionless laboratory. But do they employ this strategy when orienting movements are triggered by peripheral novel stimuli? More specifically, does it represent a collicularly dependent orienting movement? This question should be studied directly by recording the eye and head movements of cats elicited by optimal

collicular stimuli, i.e., sudden, novel distractors which release the cat's orienting reflex. There is as yet insufficient data to answer this question, but it serves as a reminder that the "stimulus problem" discussed previously is relevant to our understanding of the motor role of the SC. Whatever the role of gaze staircases in cat orienting behavior, cats are capable of executing large gaze shifts of a least 60^0 with a swift, unitary eye-head saccade (Roucoux et al., 1980), similar to those evoked by stimulation of more posterior collicular sites. The rapidity of these gaze shifts recommends them as candidates for the collicularly elicited orienting reflex. The existence of these eye-head saccades brings most of the cat's visual field within reach of unitary, targetting eye-head movements.

Roucoux et al. (1980) finally describe a region at the extreme postero-lateral margin of the SC that appears to be involved in orienting to even more extreme peripheral targets, reached by combined eye, head, and body movements. Although characterization of this zone is still at a preliminary stage, it should be noted that mammals with frontally placed eyes orient to auditory and somatosensory distractors in spatial locations beyond the peripheral limits of the visual field. This third zone may in part be involved in the control of such orienting movements. The differentiation of the collicular topography along its antero-posterior dimension appropriate for the control of the full range of gaze shifts strengthens the case for its involvement in the full orienting reflex, though there is still disagreement on the particulars of this functional differentiation.

The issues associated with collicular control of orienting movements are intimately related to the question of "frames of reference", that is, retinotopic, "craniotopic" (head centered), and bodycentered spatial coordinate systems within which sensory information is translated into motor output. When only visually elicited eye movements within the limits of ocular motility are considered, a retinotopic scheme, in principle, suffices to move the fovea onto single visual targets (Schiller & Koerner, 1971; Schiller & Stryker, 1972; Robinson, 1972). The "foveation hypothesis" postulates that a retinal error signal specifying the angular distance and direction of a target relative to the fovea is converted, via matched visual and motor collicular maps, to a motor signal that moves the visual axis of the eye through the same angular distance and direction, resulting in foveal acquisition of the target. Considerable empirical support for such a model has been gathered by recording and stimulation in the superior colliculus (Apter, 1946; Schiller & Stryker, 1972, Robinson, 1972), epitomized by the eye-position invariant coincidence of the retinal receptive field and "movement field" of saccade-related neurons below the superficial grey (Schiller & Stryker, 1972).

Recently, this conception has been challenged by findings obtained in monkeys trained to make saccades to multiple targets, which clearly demonstrate the ability of monkeys to execute saccades to spatial locations for which there is no retinal target, or for which the retinal target would generate the wrong saccade unless eye position enters the specification of saccade size and direction (Mays & Sparks, 1980).

Although a number of single unit types recorded in the colliculus in these experiments have characteristics that would allow them to serve as elements in the programming of saccades taking eye position into account, the bearing of this evidence on collicular function is, unfortunately, indirect because monkeys trained to fixate targets retain this capacity after collicular lesions (Wurtz & Goldberg, 1972; Schiller et. al., 1979). Nevertheless, the results of Mays & Sparks (1980) have reopened the question of the collicular "frame of reference" even for visually elicited saccades within the monkey's range of ocular motility.

For the colliculus as a whole it should be obvious from the preceding discussion that a retinocentric model is inadequate. Not only is a retinocentric mechanism without reference to eye position incapable of programming targetting head movements, but the additional constraints derived from collicular involvement in orienting elicited by auditory and somatosensory stimuli (Sprague & Miekle, 1966) force a consideration of alternative frames of reference.

Roucoux et al. (1980) have suggested that the anteroposterior differentiation of the collicular topography defined by the effects of electrical stimulation is synonymous with an anteroposterior succession of three coordinate systems: a retinal, a head centered, and a body centered frame of reference. The strongest evidence for this claim is the elicitation of "goal-directed" saccades from the intermediate zone, that is, saccades in a head centered coordinate system that move the eye to a fixed position in the orbit from any initial eye position. Hyde and Eason (1959) and Straschill & Rieger (1973) have also elicited

such eye movements by collicular stimulation in the cat, but others have been unable to confirm these findings (Stein et al., 1976; Harris, 1980). It should be noted, however, that all saccades illustrated or discussed directly in the report of Stein et al. were less than 7^{o} in amplitude, and therefore must have been evoked from the anterior collicular zone from which Roucoux et al. also obtain retinocentric saccades. This is not true of the results of Harris, who stimulated posterior sites, but he also is less categorical in rejecting the possibility of goal-directed eye movements, being unable to dismiss "the possibility of the eye adopting a very loose goal in the orbit". In view of the excellent documentation included in the report of Roucoux et al. (1980), the claim for goal-directed eye movements (in a head centered frame) must be taken seriously, particularly because no purely retinocentric scheme is capable of giving a coherent account of gaze shifts in an animal with a 25^{o} oculomotor range and a visual field extending to 100^{o} eccentricity.

A progression of frames of reference across the collicular topography nevertheless leaves a number of questions unanswered, specifically in relation to collicular mediation of orienting elicited by auditory and somatosensory stimuli. Physiological recording has established a rough registration of visual, auditory, and somatosensory maps in the colliculus (Gordon, 1973; Dräger & Hubel, 1975; Stein et al., 1976). The topography of these maps appears to be respected throughout the connectivity relations of the SC. For example, the somatosensory representation of the forelimb is located in the posterolateral margin of the colliculus (Stein et al., 1976) which receives the forelimb pro-

jection from both sensory and motor neocortex (Caviness, pers. comm.). It is also the collicular region selectively giving rise to the tectospinal projection to the cervical segments controlling the forelimb in contrast to the broader distribution of collicular cells projecting to cervical regions controlling neck muscles (Murray et al., 1978).

The functional, as opposed to anatomical, registration of these maps can, in the absence of additional assumptions, obtain only when the eyes and the head are in their primary position. For other eye and head positions accurate registration between the visual map on the one hand and the auditory as well as trigeminal portion of the somatosensory map on the other, would require mediation via an eye-position signal operating as a "mapshifter", whereas an additional head position signal in an analogous role would be expected to intervene between the rest of the somatosensory topography and the auditory plus trigeminal maps. That is, the already head centered auditory/trigeminal representation provides a convenient "middle ground" to which other representations can be referred with minimal expenditure on "mapshifting" schemes or their computational equivalent. Even this scheme, however, assumes a standard body posture below the neck. The laminar distribution of modalities through the depth of the SC (Edwards, 1980; Sherman et al., 1978) might lend itself to the intervention of some such "mapshifting" arrangements. There is, however, no direct evidence for their existence, unless one regards the report by Bisti et al. (1974) on vestibular modulation of visual responsiveness of superficial grey cells as relevant to this issue. In view of the tenuous evidence for the widely assumed

direct connections between the superficial grey and deeper collicular laminae (see next section), the bearing of this finding on the functional relationship between the sensory maps in the deeper strata is unknown.

A global, head-centered orienting space suggested solely on grounds of functional economy as a solution to the problem of registration of collicular sensory maps (above) may appear to be in conflict with the partite scheme of Roucoux et al. (1980). It should be noted, however, tri- that their proposal was based on stimulation evidence, and therefore is likely to reflect primarily the motor organization of collicular output. The motor strategies of the orienting reflex must involve control and coordination of eye, head, and trunk movements, as already discussed. The manner in which sensory information gains access to such control is as yet an open question. An answer will require more extensive physiological studies where the relevant postural variables are systematically manipulated, as well as behavioral assessment of the actual localization ability of a given species under varied eye, head, and body positions (see Whittington & Hepp-Raymond, 1981). The dependence of such localization on the SC would also have to be demonstrated. Awaiting the outcome of such studies, one may nevertheless summarize the preceding discussion of the motor role of the SC in the words of Roucoux et al. (1980) as follows:

> The superior colliculus, though not the only source of central saccadic command..., appears throughout the phylogenetic scale as a structure intimately involved in the control of gaze. It evolved in parallel with the progressive

> refinement of the retina, itself requiring a larger and more precise mobility of the eyeball in its socket as well as the head on the trunk. Retaining the same function, the SC acquired progressive control of the body, the head, and lastly, eye movement. Species differences in collicular function merely reflect this evolution.

The present hypothesis of collicular function places this statement within a more specific functional context: the balance of the evidence reviewed above indicates that collicular control of gaze in mammals is associated with all the overt components of the orienting reflex. According to the sentinel hypothesis the SC exercises this control over behavior, i.e., triggers the orienting reflex, in response to a limited domain of information, namely the set of distractors, and in addition commands escape in response to threat.

6. The generality of the sentinel hypothesis.

In this final section, several issues relevant to defining the range of phenomena covered by the sentinel hypothesis will be addressed. As has been stated repeatedly, the sentinel hypothesis proposes a <u>core</u> behavioral role for the superior colliculus in mammals generally, i.e., a behavioral function it exercises by virtue of the structural and functional characteristics of collicular organization shared by all mammals. It is therefore a hypothesis about the minimal and irreducible functional role of the mammalian SC. It specifies what is uniquely

"collicular" about its contribution to the total economy of sensorimotor processes across mammals, namely the sentinel role of triggering orienting and escape in response to distractors and threats. It predicts only what behavioral capacity must be lost after collicular removal in a mammal, not what in addition might be lost in a given species (see below).

What, then, are those features of the SC that lead to an expectation that there should indeed be a common functional role exercised by this structure? The SC, being a midbrain structure, shares with the rest of the brainstem a morphological and connective conservatism which preserves the basic features of collicular organization across mammalian species. Outstanding among these is the unique collicular arrangement, mentioned in the introductory sentence of this dissertation, of a superimposition of topographically organized visual, auditory, and somatosensory maps in a laminar fashion through the depth of the SC. These topographies are laid out parallel to the collicular surface in such a manner that roughly corresponding points in space represented on these maps are found along lines running perpendicular to the collicular surface (Gordon, 1973; Dräger & Hubel, 1975; Stein et al., 1976; Sherman et al., 1978). The efferent organization of the SC also appears to follow these spatial "lines of projection", because stimulation points along electrode tracks perpendicular to the collicular surface elicit similar motor effects (see, e.g., Robinson, 1972). The issues associated with registration of the sensory maps within this efferent framework for other than the primary eye and head position were considered in the previous section

of this Discussion. In view of this basic multimodal sensory-motor arrangement, which as far as is known is not duplicated by any other structure in the brain, one might ask the obvious question: What functional capacity relevant to a common motor output do the three exteroceptive modalities share?

The only functional property the three modalities have in common is their capacity to define loci in space, from the site of proximal impingement on the body surface in the case of somesthesis, to the location of visual events as far as the eye can see in the case of vision. The only universal behavioral responses triggered by spatially defined stimulus events common to all three modalities are orienting, escape, and freezing responses. Reaching behavior, for example, is not triggered by a purely auditory stimulus (though such a response might be induced by training), nor is it evoked by collicular stimulation, yet the orienting reflex is exquisitely sensitive to this type of information (Thompson & Bettinger, 1970). Similarly, locomotor approach to spatial targets is not triggered by the somatosensory system (nor by collicular stimulation), but the somesthetic system is an effective initiator of orienting and escape responses. The most characteristic feature of the mammalian SC, i.e., the superposition of the three modalities within a common efferent framework, therefore by itself recommends the SC as the prime structural candidate for central, multimodal control of orienting and escape behavior.

The laminar juxtaposition of the three modalities in a common output framework might also provide a convenient arrangement for

weighting inputs from diverse sources with respect to their efficacy in capturing the gaze. First, the prominence with which different modalities are represented in the SC might reflect the relative importance of these modalities in controlling the natural orienting and escape behavior of a given species. Secondly, summation of afference from more than one modality (e.g. vision and audition) might occur along the "lines of projection", resulting in an increase in the probability of an orienting or escape response to spatially matched multimodal information. Finally, if global inhibitory processes operate across the lines of projection, i.e., if widely separated points of the collicular topography inhibit each other, the SC would have the capacity to select one of many competing stimuli as the target for an orienting movement. Strong evidence for the operation of such global inhibition in the SC has been provided by Rizolatti et al. (1974). The same features of collicular organization that recommend its involvement in multimodal control of orienting and escape behavior, therefore provide a convenient framework for mechanisms of target selection.

The further restriction of the core, or universal, role of the SC to spontaneous orienting and escape behavior triggered by distractors and threats, i.e., to the orienting reflex proper, and its homologue in the domain of escape behavior, follows from the ready habituability of the sensory responses of collicular units below the superficial grey (close to the output stage of collicular organization), from the role of arousal in collicular function, and from the fact that the SC triggers all the overt, species-specific motor components of the

orienting reflex, as well as escape behavior. It should be noted that in the study of Horn & Hill (1966) individual units in the rabbit SC shared many of the characteristics of behavioral habituation of the orienting reflex, except that of dishabituation of the response to one stimulus caused by interpolation of a different stimulus. The animals were, however, anesthetized and did not orient in response to stimulation, which might account for the difference. All of the above circumstances receive a coherent interpretation through the sentinel hypothesis of collicular function in mammals, which provides a functional conception of the role of the SC within which each plays a necessary part.

The proposed core role of the SC common to all mammals does not by itself specify the relative weight of the collicular contribution to the total economy of sensori-motor processes in a given species. Although the SC itself is structurally conservative in mammals, this is not true of the brain as a whole. The forebrain, in particular, exhibits dramatic differences across mammalian orders and species, both as regards its relative size and anatomical complexity. Thus, in the hamster the volume of the superficial gray layer of the SC exceeds that of the dorsal lateral geniculate nucleus by a factor of three, whereas in the rhesus monkey the superficial gray has only about one-seventh of the volume of the geniculate (G.E. Schneider unpublished data). Such differences ought to be reflected in the relative weight of the collicular contribution to behavior in different species. It is, for example, conceivable that the smaller the relative size of the SC is in a given species, i.e., the more developed its forebrain sensori-

motor structures are, the more purely and exclusively is the sentinel function of the SC expressed in that species. On the other hand, in species such as rodents, the tree shrew, and the ground squirrel, whose colliculus is relatively large compared to forebrain sensorimotor structures, the collicular contribution to behavior might appear to extend beyond the role specified by the sentinel hypothesis.

If for no other reason than the prominent collicular projections to the brain stem reticular formation (see Edwards, 1980), collicular removal in species with high "colliculus/forebrain ratios" may be expected to have proportionally greater disruptive consequences for the functional integrity of a variety of sensorimotor processes which themselves are not directly mediated by collicular circuitry. A particularly dramatic example of this class of effects has recently been reported by Schiller et al. (1979). Neither the frontal eye fields nor the SC are themselves directly part of the neural circuitry involved in optokinetic nystagmus or the vestibulo-ocular reflex, yet their combined removal in the monkey leads to drastic deficits in all ocular motility, extending to eye movements evoked by optokinetic and vestibular stimulation. This unexpected result is most readily interpretable as the effect of an incapacitating disfacilitation of basic brain stem oculomotor circuitry resulting from the removal of two of its normal inputs. It would therefore not be surprising to find that collicular removal by itself, in species with a much highter colliculus/forebrain (or why not colliculus/frontal eye field) ratio than the monkey, might disable sensorimotor functions not directly mediated by collicular circuitry.

Such an effect might provide at least one possible explanation for deficits in reinforced orienting movements in colliculectomized hamsters (Schneider, 1967, 1969) and tree shrews (Casagrande & Diamond, 1974), obtained in food-perimetry situations, for which the sentinel hypothesis does not predict a permanent collicular deficit.

Food perimetry in animal visual field testing represents an adaptation of visual field perimetry in humans, where the verbal response of the patient ("yes, I saw it") is replaced by an orienting response to the stimulus on the part of the animal. Because all such responses habituate rapidly, they must be maintained by extrinsically motivating the animal with food or water reward. It seems highly unlikely that any brain structure has evolved under this type of selection pressure in nature. Orienting responses to suddenly appearing stimuli are simply not a prominent part of the food-getting behavior of most mammals. It may indeed happen that a seed drops somewhere near a hamster wandering through a Syrian wheat field. If so, the collicular sentinel would trigger an orienting movement, and that would be the end of its involvement in hamster food-getting. Fortunately hamsters do not wait for seeds to drop in their vicinity, they purposively forage for them, and even fell wheat stalks by gnawing at their base. According to the present perspective, the SC plays no crucial role in these type of activities - rather, it protects the hamster from the unforeseen during his familiar foraging rounds, and only rarely does the unforeseen turn out to be food.

In view of the above, deficits in reinforced orienting to stimuli

are difficult to interpret in terms of natural categories of sensorimotor function. The mammalian orienting reflex is driven by novelty. Even in the laboratory, when reinforced orienting movements are put into competition with novel distractors, the latter invariably "win", i.e. capture the gaze (provided the animal has an intact SC, see Albano & Wurtz, 1978), because response to distraction is the natural functional domain of the mammalian orienting reflex. The pattern of eye-head coordination may even differ for orienting triggered by novel versus reinforced stimuli, as noted in connection with the high velocity combined eye-head saccades in cats reported by Roucoux et al. (1980). However this may be, impairments in reinforced orienting movements after brain lesions may be attributable to deficits in the motivational, memory, sensory, motor, or arousal components of the behavioral act. They therefore allow no direct inferences about the functional role of the damaged structure unless these factors are varied independently or controlled for.

From the present point of view the discrepancy between the observations of Schneider (1967, 1969) and Mort et al. (1980) on the effects of collicular undercutting on reinforced orienting movements to sunflower seeds in a "food perimetry" situation is therefore a minor issue. Procedural differences affecting any of the above-mentioned variables relevant to reinforced orienting might account for the contrast between the drastic deficits found by the former, and the considerable sparing of orienting ability seen by the latter in what appear to be comparable lesion cases. To reiterate: food-perimetric procedures do not tap

natural categories of sensorimotor function in mammals, and are affected by too many variables to permit straight-forward inferences about the role of a structure in orienting behavior.

The total and permanent deficits in reinforced orienting observed by Schneider in his most complete collicular undercuts are most easily reconciled with a strict reading of the sentinel hypothesis if interpreted as the result of disfacilitation of noncollicular circuitry by collicular removal, by analogy to the findings of Schiller et al., referred to above. The rough correspondance between visual field regions exhibiting partial sparing or recovery of reinforced orienting and collicular regions spared in cases with less complete undercuts in Schneider's study is compatible with this interpretation. The most likely site of convergence between collicular and noncollicular pathways for orienting behavior is the brain stem and cervical preoculomotor and cephalogyric apparatus, where collicular input must maintain an organization appropriate to the demands of the motor system. In animals such as the hamster, the collicular input to these structures is likely to be prominent in comparison with that of other systems, and hence might be expected to have a correspondingly important role in maintaining the functional integrity of the converging pathways.

After this interpretation it may be argued that the "wrong direction turning" of hamsters with a neonatally induced aberrant retinal projection to the ipsilateral SC (Schneider, 1970, 1973, 1975, 1979) constitutes strong evidence for direct collicular mediation of reinforced orienting in the hamster. It should be noted, however, that the be-

havioral results in such cases are extremely variable, perhaps an inevitable consequence of the abnormal innervation of the colliculus in such cases. For example, some cases with neonatal removal of one eye show a larger, and others a smaller, visual field region capable of eliciting "wrong direction turns" than cases without such eye removal, despite the fact that the eye removal induces a far greater misinnervation of the spared colliculus than when both eyes are left intact. The wrong direction turns themselves are quite variable, and do not terminate in the mirrow-image positions predicted by the visual field representation in the aberrantly innervated colliculus. They are often terminated at the point where the stimulus leaves the visual field. This observation, and the fact that exclusively wrong way turns are elicited only from a small region of the upper temporal visual field, i.e., from within the region of the hamster visual field that appears preferentially involved in escape behavior, opens the possibility that "wrong direction turns" might instead be "correct direction avoidance" of a disturbing stimulus.

If reinforced orienting is in fact mediated by a noncollicular system, commanding a correct turn in "rewired" hamsters, this system would be receiving what is in all probability a suboptimal or abnormally patterned facilitation from the lesioned colliculus, where retinal fibers grow into the remaining deeper layers. This not quite normal command for a correct turn would at the same time come into conflict with collicular facilitation of the contralateral brain stem circuitry, originating in the intact colliculus innervated by the re-

crossing projection from the retina. Similar "conflict effects" would obtain at all sites where collicular projections interact with the rest of the visual system, including forebrain targets of collicular efferents. If such a situation is somehow aversive to a hamster, the animal might very well attempt to turn away from the stimulus inducing the conflict. The goal of this avoidance would be reached at the point where the stimulus leaves the visual field. Both the "curing" effect of transsecting the recrossing bundle, and the "unmasking" effects of undercutting the residual lesioned colliculus (see Schneider, 1979) are compatible with this interpretation. This admittedly speculative interpretation of "wrong direction turning" would have to be eliminated before the turning behavior of hamsters with a recrossing projection to the SC can be considered direct evidence for an obligatory role of the hamster SC in reinforced orienting movements.

Besides the hamster, the tree shrew has been reported to lose all reinforced orienting movements in a food perimetry situation, except in a narrow frontal sector of the visual field, after deep collicular lesions (Casagrande & Diamond, 1974). The tree shrew has an enormously developed SC, both as regards size and anatomical differentiation. This may make the "disfacilitation" interpretation proposed above relevant to this deficit as well, though in this species additional factors should be considered. The tree shrew is one of those mammals that actually use rapid series of orienting movements as an intergral part of their food-getting behavior. The animal is an insectivore, and pursues flying insects (houseflies, butterflies, moths, bees, dragon

flies) in explosive, high-speed chases, leaping into the air to catch the insect with its mouth in mid-flight (unpublished, filmed, observations by the present author). It therefore seems possible, even plausible, that the collicular control over the orienting reflex has been incorporated directly into the control of the impressive pursuit behavior of this species. This might account, in part, for its extreme collicular development as well as the devastating effects of collicular removal in the tree shrew, which, parenthetically, include abolition of escape to visual threat (see Casagrande & Diamond, 1974).

A comparison of tree shrew and squirrel orienting behavior after SC lesions might be informative with respect to the above proposal. Both species have evolved in a similar habitat, but only the former engages in lightning pursuit of insects. The latter collects nuts. Finally, it should be noted that the tree shrew is also the "sentinel animal par excellance". Its alertness, caution, and attentiveness to minute changes in its surroundings, persists through years of familiarity with a single environment. This acute sensitivity of tree shrew "sentinel functions" is expected from the present point of view, because of the extreme development of the SC in this species.

A final behavioral issue requires comment because of its problematic relation to the sentinel hypothesis. Do spatially nonspecific override responses, such as the essentially defensive responses of startle, freezing, and arrest, fall within the output range of the SC? They seem closely allied with orienting and escape behavior by overriding ongoing behavior in response to a subset of the same stimulus

domain proposed to activate the collicular sentinel, yet differ from the distraction and escape responses of the present study by resulting in simple arrest or cessation of ongoing behavior, rather than its spatial redirection.

There appear to be primarily two situations in which animals respond to novelty by arrest or freezing. One is exposure to global novelty, i.e., situations in which novelty surrounds the animal completely, or impinges on it in such a way that its spatial source is impossible to determine. This makes all orienting movements equally appropriate for gathering relevant information, and makes maintenance of the initial position in which the animal encounters the situation, i.e., arrest, the optimal response, particularly since movement may enhance the animal's visibility to potential predators lurking in the global novelty. The other situation is one in which a stimulus normally would trigger escape, but in which the animal has no known routes of escape or safe havens. This situation is most likely to occur in combination with that of global novelty, such as on the introduction of an animal into an open field for the first time. In that situation initial freezing is a highly probable response (see, e.g., Bindra, 1959).

It is easy to imagine a scheme according to which the SC, normally overriding ongoing behavior with orienting or escape responses to spatially defined novel stimuli, might simply arrest behavior when the eliciting novelty is distributed throughout the animal's sensory field. Yet collicular single units do not appear to be particularly sensitive to wide-field stimuli, and it is as easy to imagine that

structures that do possess such unit responsiveness mediate the arrest and freezing responses at issue here. Behavioral evidence on collicular mediation of arrest reactions to global novelty would have to be obtained in animals with very complete collicular lesions that did not encroach on alternate candidate structures, such as the pretectum. The specific conditions of testing might also influence the outcome, as suggested by the finding of Goodale et al. (1975) that startle to intense stimuli in colliculectomized rats is deficient only when competing with active ongoing behavior such as grooming or sniffing, but not at times when the animal has no obvious focus of behavioral activity. In view of these complicating factors, the dependence of essentially defensive, spatially non-specific override responses on the SC in mammals will have to be determined by further empirical studies taking these factors into account.

A final issue that requires comment with respect to the generality of the sentinel hypothesis concerns the anatomical localization of collicular sentinel functions. Mounting anatomical and functional evidence points to drastic differences between, and even independence of, the superficial grey substance of the SC and the laminae lying beneath it. This issue was first brought into clear focus by the behavioral results of Casagrande & Diamond (1974). Ablation of the tree shrew's superficial grey alone produced deficits on certain visual discrimination tasks, but did not substantially impair visually elicited orienting behavior. The latter was dramatically impaired only after lesions which in addition destroyed the underlying layers of

the SC. The interpretation of these results as evidence for two collicular "organs", proposed by the above authors, has since received considerable support.

Edwards (1980) has recently emphasized the marked differences in connective relations between the superficial grey portion of the SC and the rest of that structure. It is the deeper layers that are profusely interconnected with subcortical and cortical structures in several modalities, and give rise to all descending collicular efferents. The superficial grey, on the other hand, appears related exclusively to visual structures, and forebrain visual structures in particular, both in its afferent and efferent relations. Because the parabigeminal nucleus (the only brain stem target of the superficial grey besides the pretectum) appears to form a closed "satellite system" of the superficial grey (Graybiel, 1978), the only connections of the superficial grey that do not lead to the forebrain are those with the pretectum. Conspicuously absent from the well documented connections of the superficial grey is the nearly universally assumed projection to the underlying deeper layers of the SC, a circumstance poignantly established in the paper by Edwards cited above. All fiber degeneration or label seen in deeper laminae after superficial lesions or amino acid injections may be due to the prominent fiber projection destined for the parabigeminal nucleus. The burden of proof has therefore shifted onto those who assume that a direct synaptic linkage between superficial and deeper colliculus exists. Indirect linkages via, say, dendrodendritic routes of influence are of course not ex-

cluded by this state of affairs.

A number of functional properties of the SC are more easily understood once the presumed obligatory linkage between the superficial grey and deeper colliculus is broken. The behavioral findings of Casagrande and Diamond have already been mentioned. Another is the drastically elevated thresholds for evoking eye movements by direct electrical stimulation of the superficial colliculus, compared to deeper stimulation sites. Current thresholds may be one to two orders of magnitude higher at superficial sites (Robinson, 1972; Schiller & Stryker, 1972; Roucoux et al., 1980), which is hardly what one would expect if superficial grey cells exert direct synaptic drive on underlying cell populations. The numerical current threshold values reported for superficial stimulation sites are compatible with excitation of a fixed population of output cells beneath the superficial grey by direct current spread, according to the current-distance relations published by Stoney et al. (1968) and Ranck (1975). The physiological results of Mays and Sparks (1980) further indicate a dissociation between visually induced activity in the superficial grey and the firing of saccade-related units in deeper laminae. Finally, 2-deoxyglucose autoradiographic evidence obtained in the rat indicates that unilateral eye removal induces a drastic difference in the activity level of the superficial grey on the two sides of the SC, yet is not reflected in any difference in the activity level of the underlying layers on the two sides (McCulloch et al., 1980).

Taken together these various findings converge on the conclusion

that the SC may indeed best be viewed as composed of two "organs", a visual, sensory, superficial portion related primarily to forebrain visual areas, and a "reticular", multimodal, deep portion related to a far greater extent of the neuraxis, spanning from spinal cord to diencephalon. If this is so, it immediately forces the question: for which part of the SC does the sentinel hypothesis propose a function, the superficial or deep portion? From all that has been said in this Discussion, it should be obvious that the choice is easy and clear: the sentinel hypothesis is concerned with the deeper, multimodal, reticular, easily habituable, sensori-motor portion of the SC. That is where the mammalian sentinel "lives".

The segregation of the superficial from the deeper SC is of importance for the sentinel hypothesis primarily by providing a more accurate anatomical definition of the sentinel functions of the SC. It does, of course, also imply that the functional role of the superficial grey substance has to be sought in its own right, a problem for which the sentinel hypothesis is not likely to provide much guidance. The close relationship of the superficial portion of the SC with forebrain visual areas suggests that certain aspects of the pattern analysis and discriminative functions of the forebrain visual system rely on this extrageniculate pathway through the SC in their operations. The results of Casagrande & Diamond (1974) support this view. According to the present perspective on collicular function, deficits in discrimination performance after collicular lesions are likely to result either from a role of the superficial grey in such

tasks, or from dependence of some facet of the task on the sentinel functions of the deeper collicular laminae. Which of these alternatives is most relevant to the interpretation of discrimination performance deficits obtained after collicular lesions (see, e.g., Kurtz, 1977) would have to be determined by assessing the effects of laminar collicular lesions on task performance, as done by Casagrande & Diamond (1974).

Conclusion

The central theme of this dissertation has been "what is the SC for"? The present behavioral results, supported by a number of previous finding reported in the literature, suggest that the SC does both more and less than implied by the dominant "visual grasp reflex " and "foveation" conceptions of its behavioral role. The sentinel hypothesis extends the functional domain of the SC to include a necessary role in escape away from unlearned visual threat, and constrains its role in orienting behavior directed towards stimuli to the orienting reflex proper, both in its stimulus requirements and motor expression. It proposes, in other words, that in all mammals the SC is a structure essential for mediating the species-specific orienting reflex triggered by novel (unlearned) stimuli, as well as escape reactions evoked by unlearned threats. Either of these disparate behavioral outputs of the SC (towards or away from unlearned stimuli) deflect an animal away from its current task or goal, expressed in the sentinel hypothesis as the override function of the SC. This general collicular

override function is assumed to be in dynamic competition with systems guiding ongoing (task-oriented) behavior, both motivationally and spatially. A variety of functional properties of the deeper collicular laminae receive a natural interpretation through the sentinel hypothesis, which may provide a unifying conception for the essential behavioral role of the SC (below the superficial grey) common to all mammals.

TABLE I

Categorization of stimulus events included in the arena of the present experiment

Functional type	Stimulus category	Stimulus	Location in arena
DISTRACTOR	Truly novel stationary visual	NOV L NOV R NOV L+R	ALLEY
	Transient visual distractor	VIS L VIS R VIS L+R	
	Transient auditory distractor	AUD L AUD R AUD L+R	
	Transient somatosensory distractor	SS L SS R SS L+R	
THREAT	Stationary visual threat	OVERHEAD	
	Moving visual threat	LOOM L LOOM R	OPEN FIELD
GOAL	Single aperture	APERT L APERT R	
	Multiple apertures	APERT M+L APERT M+R APERT L+R	
	Catch trial	NO APERT	

TABLE II

Ordinal position of stimulus events over trials. At least two non-stimulus trials intervene between any 2 stimulus trials.

Stimulus	Position in sequence			Extra sequence
VIS L	10	24		7
VIS R		16	42	13
VIS L+R	2		30	3
AUD L	12		36	10
AUD R		18	32	15
AUD L+R	6	26		4
SS L		22	40	11
SS R	14		38	16
SS L+R	8	28		6
NOV L			34	
NOV R		20		
NOV L+R	4			
OVERHEAD	13			12
APERT L	3	15	31	2
APERT R	1	25	33	1
APERT L+R	11	23	39	17
APERT M+L	7	19	37	14
APERT M+R	9	27	35	9
NO APERT	5	17	29	5
LOOM L			41	8
LOOM R		21		17

TABLE III

Spearman rank order correlation coefficient (r_S) for each testing condition, with its associated significance level (p) determined by one-tailed test according to Glasser & Winter (1961), and the number of data pairs (N) on which the coefficient is based.

Testing condition	r_S	P	N
Moving visual threat	.85	.001	12
Stationary vis. threat	.83	.01	8
Visual runway distractor	.72	.01	12
Truly novel stimulus	.48	NS	12
Aperture approach, total	.56	.05	12
Aperture approach, early	.63	.05	12
Aperture approach, late	.49	NS	11

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FIGURE LEGENDS

Figure 1. Nest container in its bay at back of arena. Dashed line demarcates the sectorial compartment occupied by one nest. RD, return door; LF light fixture covering exit from nest; V, entrance vestibule connecting nest exit to arena entrance; W, water vial. See text for further details (p. 17).

Figure 2. Top view of testing arena. A, alley or runway; M, maze; F, open field; ret., return alleys leading to nest container; VIS, stimulus panel of transient visual distractor (see also figure 3); AUD, loudspeaker covered with gauze cloth lid; SS, polyethylene tube for delivery of air puff serving as somatosensory stimulus; P, photobeam (see also figure 3); R, ramp ascending from maze floor; B, bridge suspended so that it flips down under animal's weight and provides exit to open field from bridge. The exit from maze to open field has been filled in with black for the sake of identification. Dottes "S" and "A", indicator lights coupled to relay activating SS and AUD stimulus events, respectively. The indicator lights are visible to the camera but not to the animal. A "middle plus left" (M+L) aperture conflict situation has been depicted in the open field.

Figure 3. "Hamster eye view" of the alley or runway. Exit to maze at center, rear. Activated visual transient distractor on the left. Activated "truly novel" stimulus depicted on the right. These two stimulus events are shown together only for the sake of convenience. During testing they would always occur on separate trials. Foreground: closest are tubes delivering somatosensory air puff, and behind them the photobeam arrangement consisting of tubes containing photoresistors. Mirror on top of each tube reflects ambient light into the opposite tube.

Figure 4. a) Map of the contralateral retina on the standard dorsal view reconstruction of the SC used in the present experiment, from Frost & Schneider, 1979. Closed curves represent isoeccentricity lines spaced 20^{o} apart, and centered on the geometric center of the eye. Radial lines represent meridia spaced 30^{o} apart. T, S, N, I: representation of temporal, superior, nasal, and inferior extremities of the retina, respectively. These points define the major axes of the eye determined by the midpoint of the attachment of the four rectus muscles. In this dorsal view reconstruction the medial surface of the SC is not visible.
b) Left: Collicular representation of the visual field of the

contralateral eye in spherical coordinates centered on "straight ahead" with respect to the hamster's head. On the assumption that the normal position of the hamster's eye is such that its optical axis points 60^{o} lateral to the head midline, and 30^{o} above the horizon (Schneider, unpublished observations), the retinal map in a) above was remapped on the collicular surface with these two coordinate transformations. H, representation of the horizontal meridian of the hamster's visual field; V, representation of the vertical meridian of the visual field, i.e., the intersection of the midsagittal plane of the head with the sphere of the visual field. Other contours spaced as in a) above.
Right: Collicular representation of visual stimulus events in the arena mapped for the head position in which the animal would normally encounter the stimuli. 1, left aperture in the open field; 2, "truly novel" stimulus in the alley mapped for the first point at which this stimulus is visible to the animal on entering the arena; 3, the transient visual runway distractor at the point where the animal breaks the photobeam; 4, the overhead stationary visual threat; dashed outlines enclose the representation of this stimulus as the animal locomotes forward from the first point at which the stimulus is visible; 5, the moving visual threat in the open field. Black: representation of the stimulus when the animal is at the center of the open field; dotted surround: representation of stimulus for other positions of the animal during locomotion towards the middle aperture. Motion of the leading edge of the stimulus is represented in the colliculus by movement along an isoeccentricity contour towards the medial edge of the SC, descending along a portion of the unrepresented medial wall.

Figure 5. Dorsal view reconstruction of the topographic pattern of collicular undercutting for animal #2. A representative series of frontal sections drawn from Nissl stained serial sections through the SC are included to illustrate the method of reconstruction (serial sections with other stains were also used to define the pattern of damage represented on the dorsal view). The undercut is drawn in heavy black. The portion of the right SC enclosed by dashed and dotted lines in sections 5 and 6 had disintegrated in vivo. See text (p. 30) for further details. Below the damaged colliculus numerical estimates of "lesion-stimulus overlap" are provided for each stimulus category (see text, p. 34). The measurements were performed directly on the reconstruction, at the scale of figures 6 through 9.

Figure 6. Dorsal view reconstruction of undercuts for animals #12 and #15. See legend for figure 5 for further details.

Figure 7. Animal #17: see legend of figure 6.
Animal # 3: dorsal view reconstruction of those regions of the SC with zero grain density above background assessed on serial sections through the SC processed autoradiographically after an eye injection of radioactively labeled amino acids 24 hours prior to perfusion. See text, p. 29, for further details.

Figure 8. Animal #4: same as legend for figure 7, animal #3.
Animal #11: this animal received a unilateral brachium cut of the left superior colliculus and underwent a full course of postoperative testing. It then received an additional brachium cut of the contralateral SC and was tested again. Because the second brachium cut extended beyond the midline the medial extent of denervation caused by the first cut could not be determined with certainty. Differences in the depth of tissue damage caused by the two stereotaxic knife cuts made it possible to establish with certainty that the second cut extended at least as far as indicated by the shading extending across the midline from the right SC. The full medial extent of the first cut has been left undetermined, as indicated by question marks along a conservatively drawn border. No data on responses to the two visual threats were therefore included in the analysis of the first lesion. After the second lesion the entire area between the left and right damage formed part of the lesion, and data for responses to the threats were included in the analysis. After the second lesion most of the right SC within the shaded area degenerated.

Figure 9. Animal #16: same legend as for figure 7, animal #3.

Figure 10. Comparison of pre- and postoperative responses to the left and right transient visual distractor. Circles with trailing dashes indicate the position of the animal's nose and the orientation of its head midline at the point of stimulus onset. A dashed orientation marker on a trajectory indicates final head position at the completion of an orienting movement to the stimulus. The dotted line crossing the runway indicates the position of the photobeam, except in the preoperative "L" panel. For these trials, which were among the earliest of the entire experiment, the position of the photobeam had not yet been finalized. This explains the scatter of initial head positions for these trials. Variance in initial head position for all other trials is caused by differences in running speed. No trials have been excluded from the diagram.

Figure 11. Comparison of pre- and postoperative approach to left and right apertures for animal #2. Each panel shows the exit of the maze, the baited aperture, the animal's head position when it first becomes visible on the film, and the "nose-trajectory" to the aperture. Postoperative trajectories have been divided into three sets (I, II, III) corresponding to trials filmed during three consecutive testing periods, each approximately 10 days long. No trials have been excluded from this summary diagram.

Figure 12. Animal #12: All pre- and postoperative responses to the "truly novel" visual distractor in the alley. All trajectories except the "Post L" are good examples of approach and exploration elicited by this stimulus. The right collicular undercut completely covers the representation of the left stimulus.
Animal #11: A representative example of vacillation and "dash" response to the overhead stationary visual threat.The last two head orientation markers on either trajectory are separated by 168msec. The postoperative trajectory was filmed after the 2nd brachium cut.

Figure 13. A comparison of responses to the moving visual threat in animal #4 and #17, which had one of the lowest and the highest predicted deficits for this stimulus category, respectively. All postoperative trials are included.

Figure 14. All "aperture conflict" trials for animal #15. Conventions are the same as for figure 11, except that one of the two apertures that were present on each trial were not included in order to save space. See text (p. 49) for a description of these responses.

Figure 15. All postoperative aperture conflict and "catch trial" trajectories, and a random sample of approaches to the middle aperture for animal #2. Conventions as in figure 14. See text (p.50) for a description of these responses.

Figure 16. All preoperative escapes to the moving visual threat for all animals. Response-trajectories to left stimuli have been mirror-imaged across the midline of the arena. The projection of the leading edge of the threat stimulus has been projected onto the arena floor at the point of its maximal intrusion into the arena. Escapes directed into the return alleys have been marked with letters representing the laterality of the eliciting stimulus. On the right hand side of the figure the same data (escapes to

left stimuli still mirror-imaged) are presented at double magnification with appended head orientation markers, dotted markers indicating position at approximately 168msec. and solid markers at twice that time after stimulus onset. The trajectories have been superimposed in such a manner that they share an identical initial head position and orientation. The 10cm calibration line bears no relation to the eliciting stimulus.

Figure 17. Bar graphs summarizing all data analysis based on the "responsiveness" measure. A figure indicating the number of animals on which the data represented by a given bar is based appears immediately below that bar, and below this number the total number of trials on which the bar is based appears. Top graph: the outcome of the analysis of habituation effects (see text, p.51). Middle graph: text, p. 51). Bottom graph: the results for the analysis of postoperative recovery (see p.53 of text).

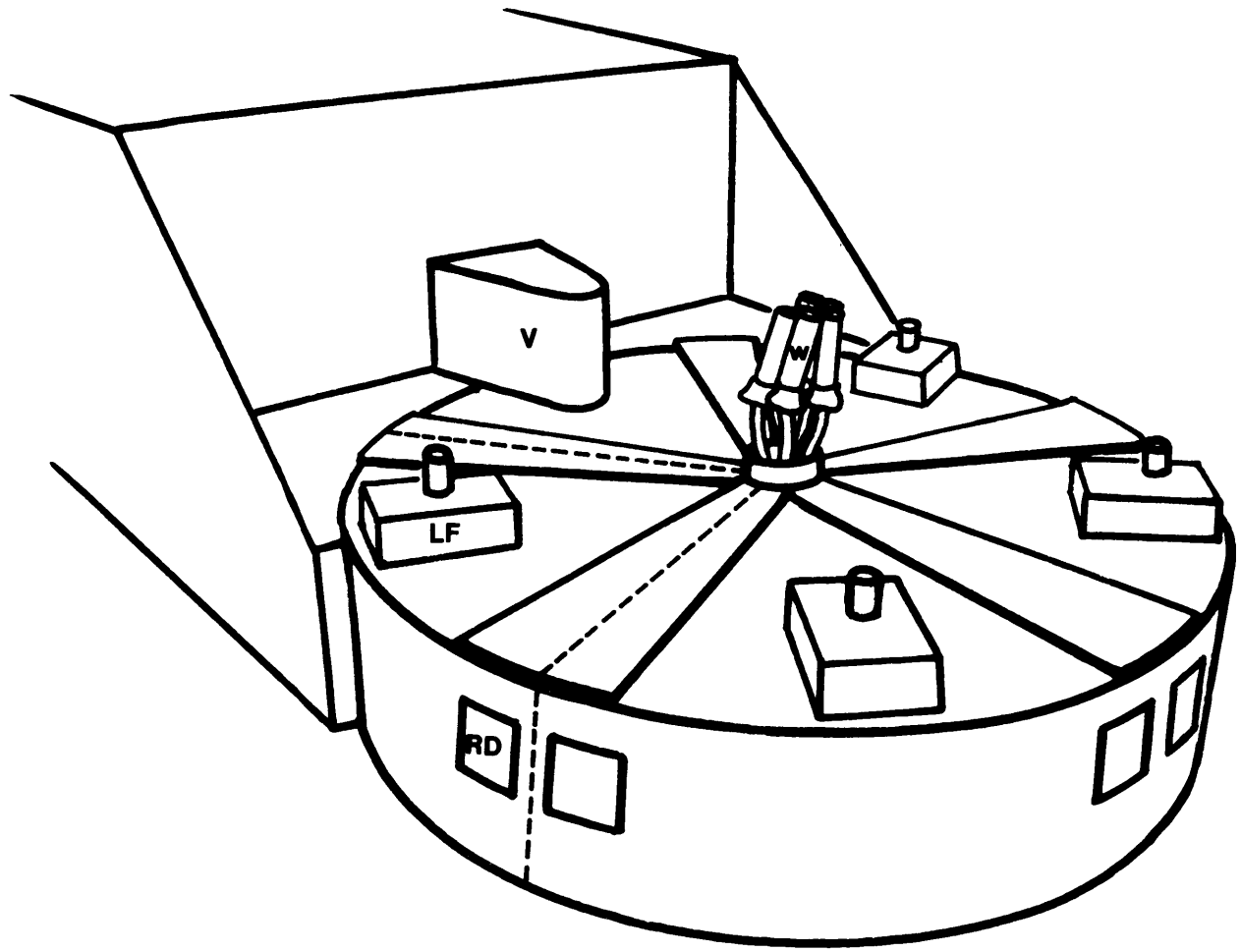


Figure 1

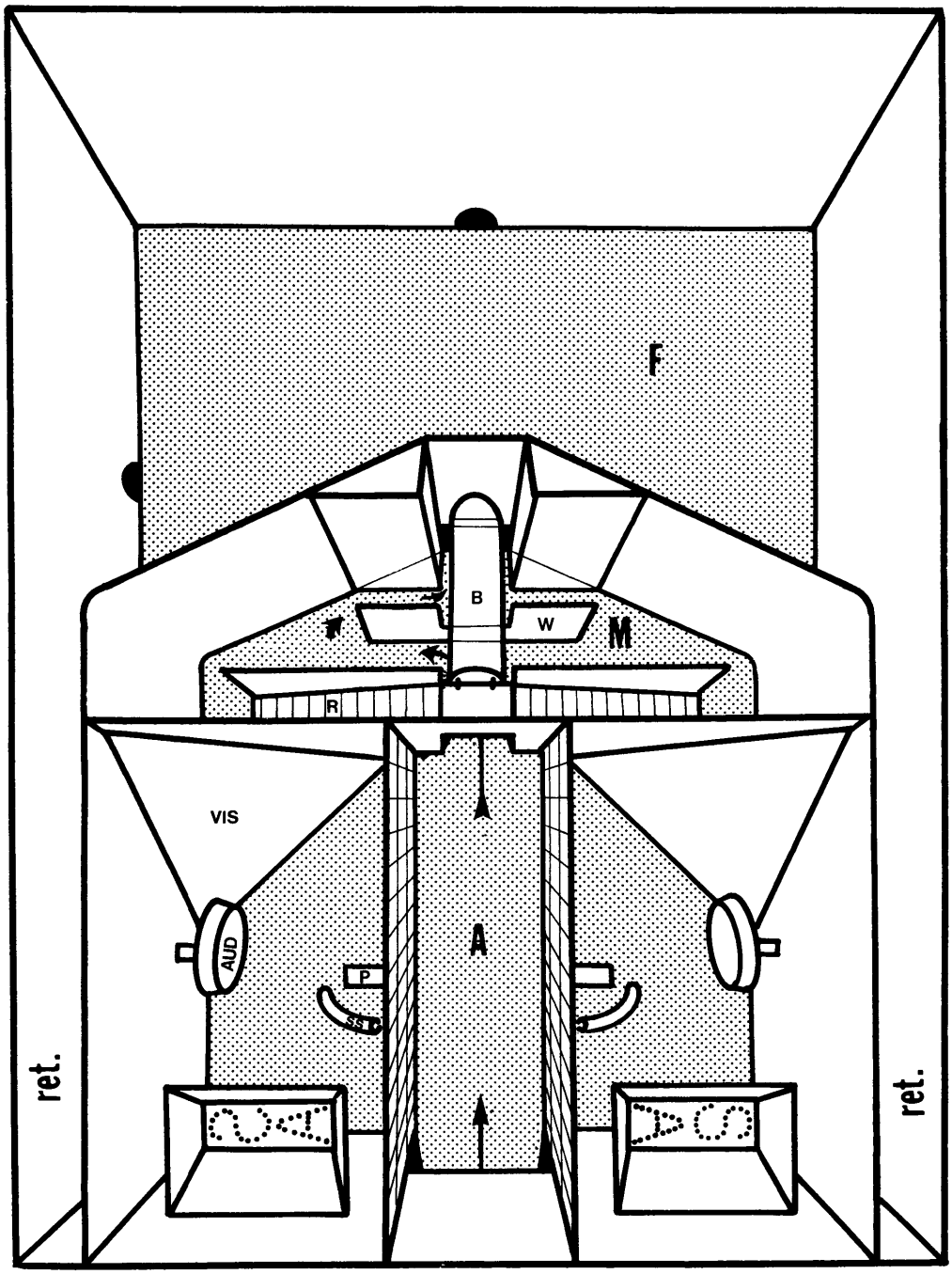


Figure 2

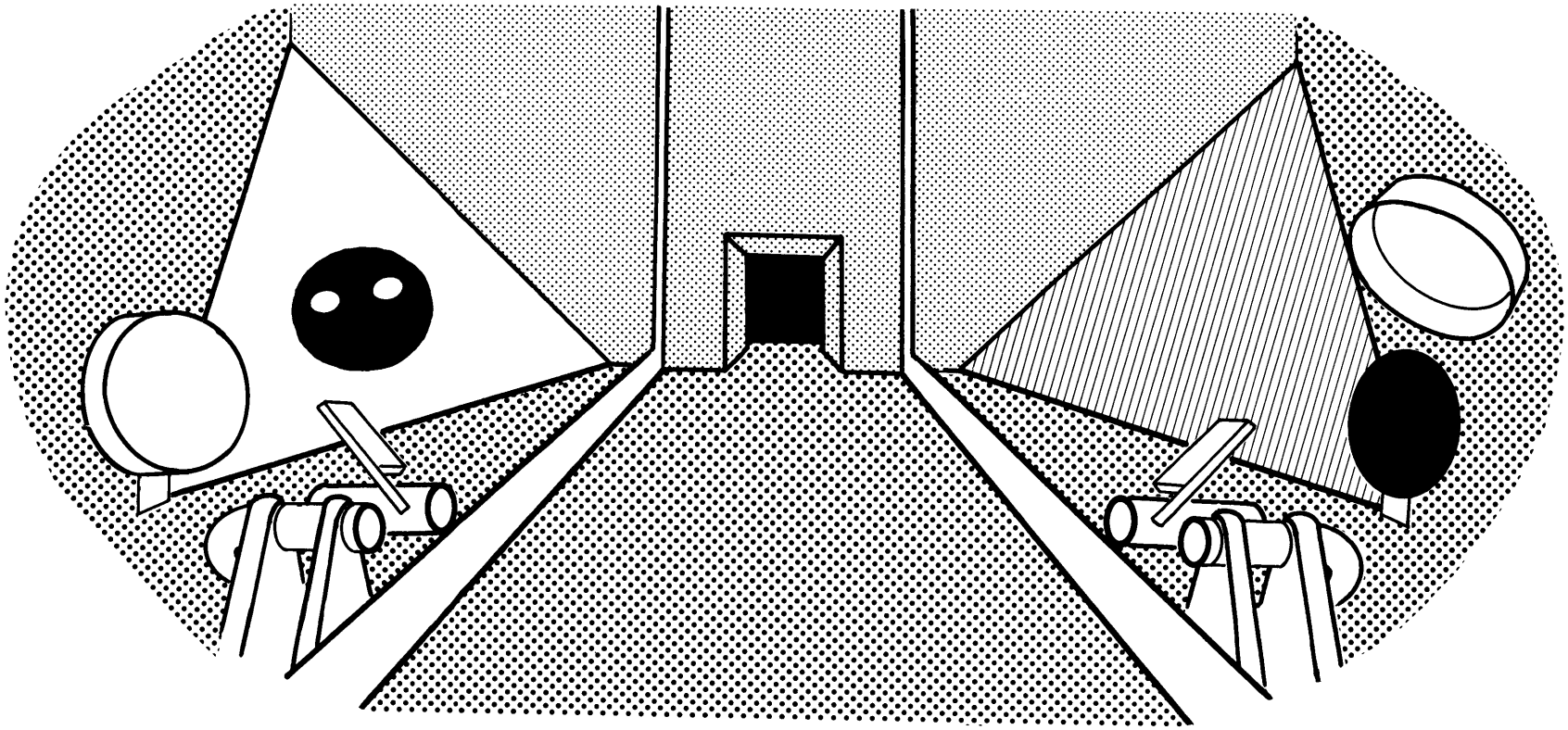
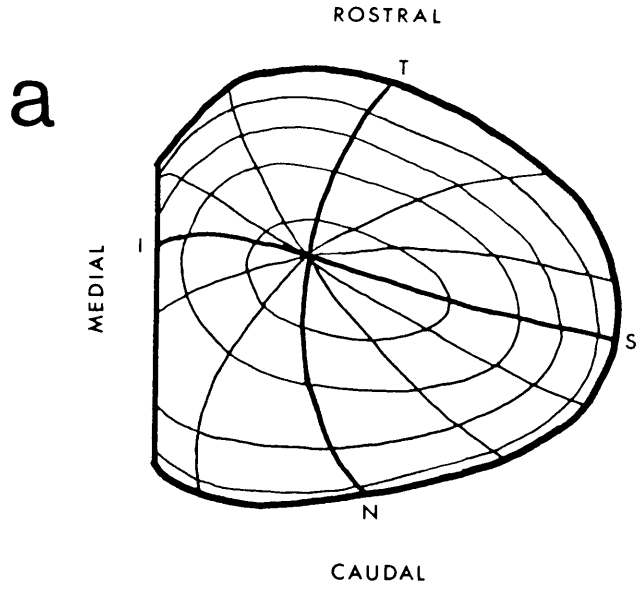


Figure 3



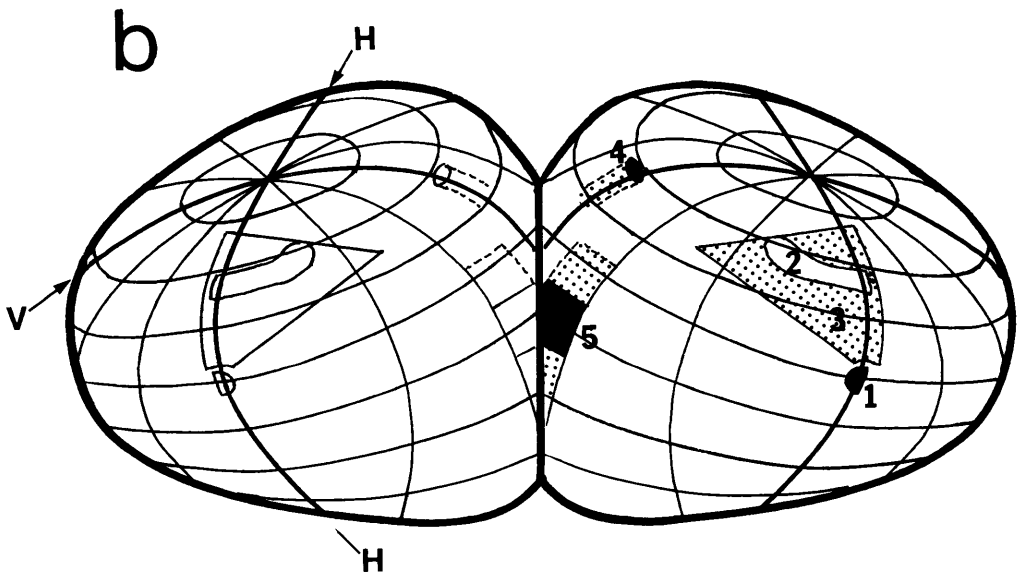


Figure 4

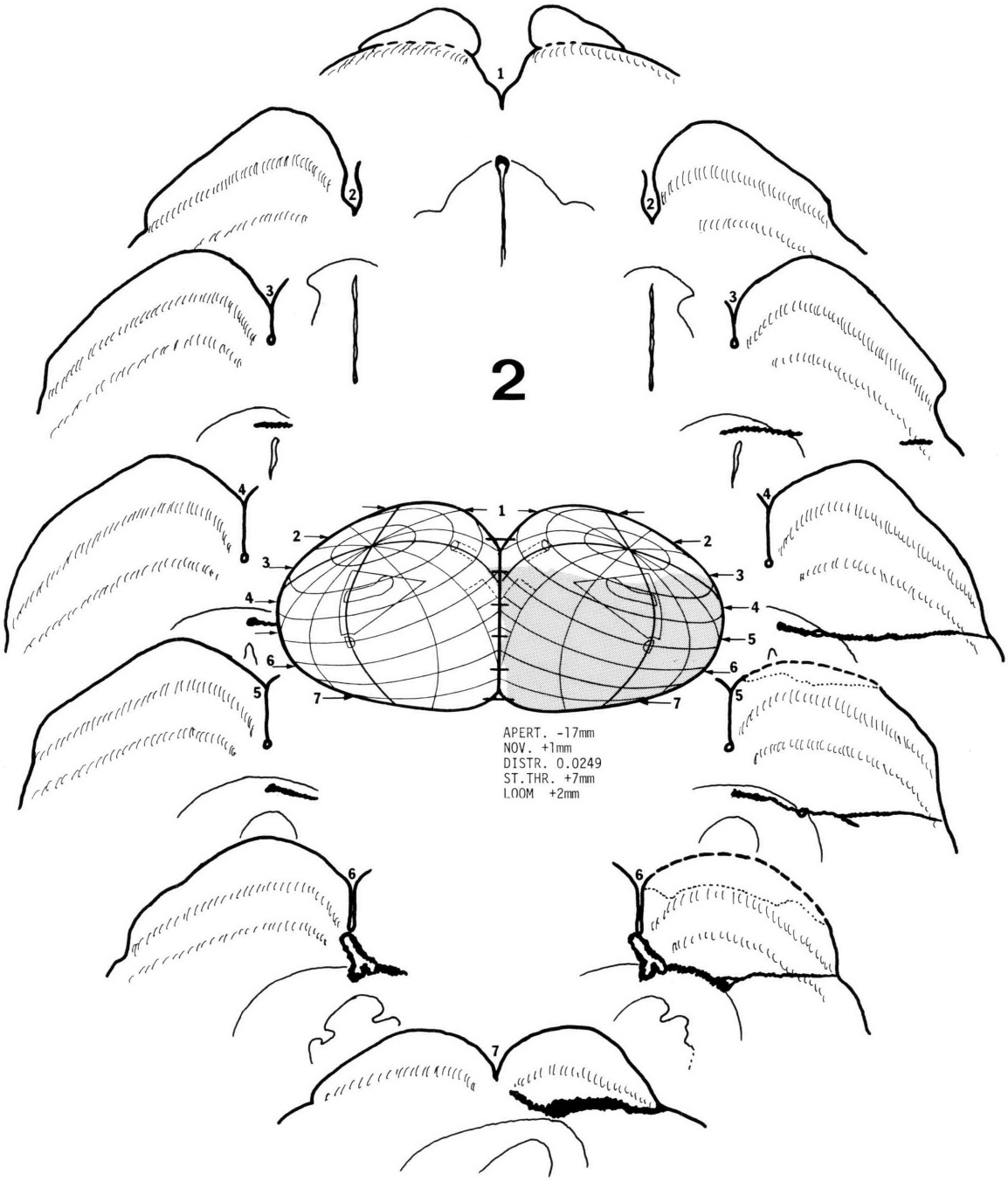
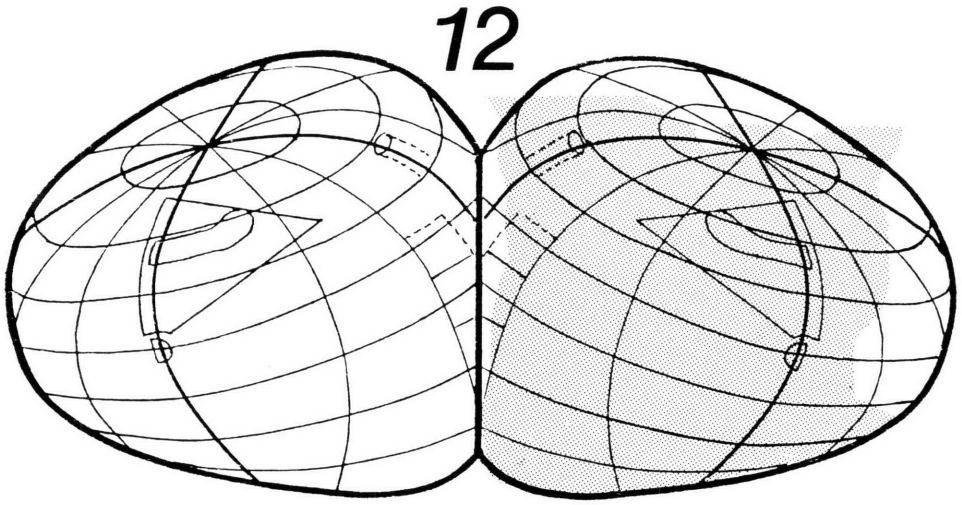


Figure 5



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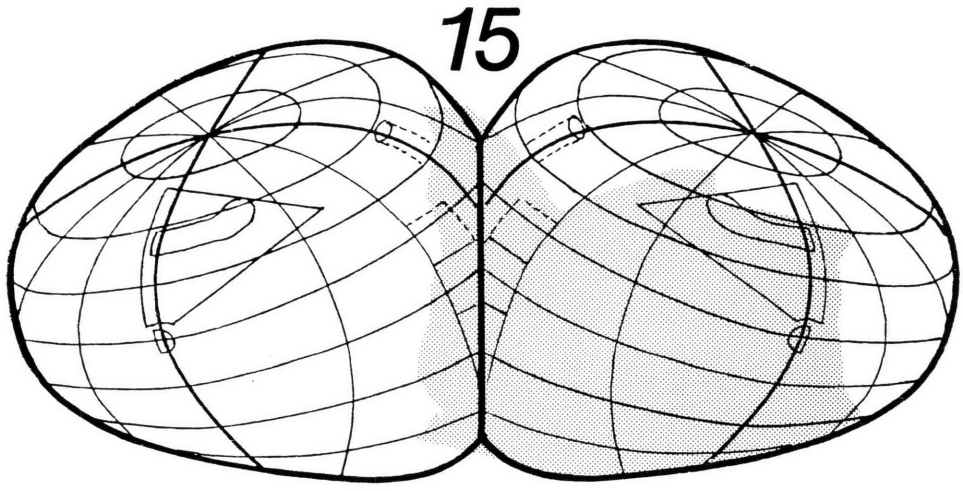

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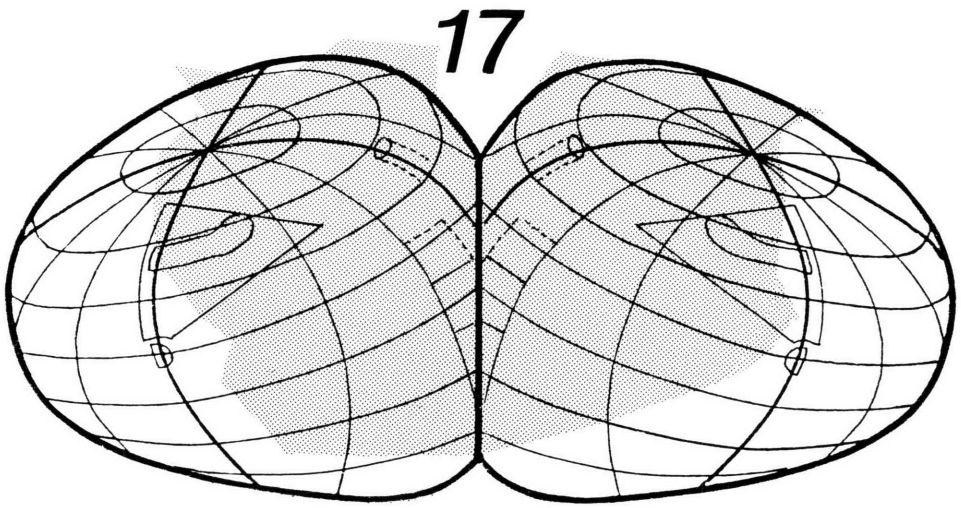
LOOM -5mm

ST.THR. +6mm
LOOM +0.5mm

Figure 6



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LOOM -27mm

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NOV. +5mm
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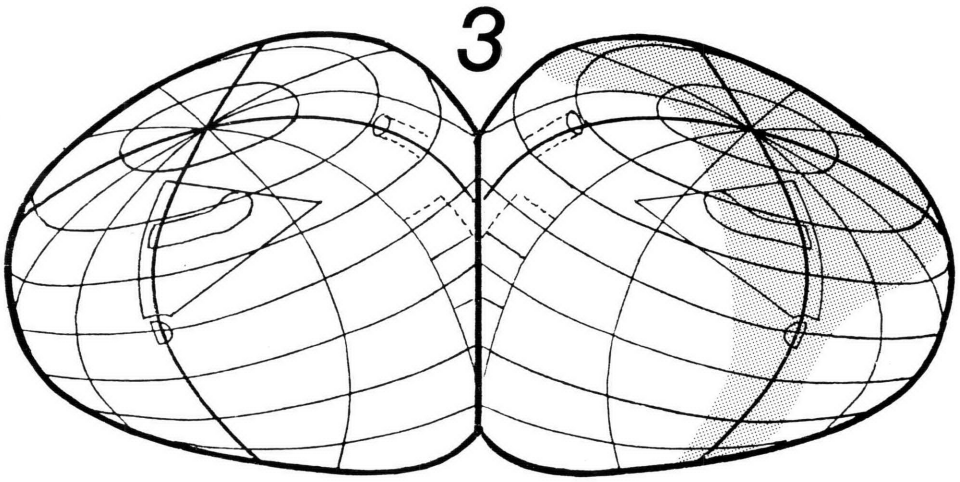
ST.THR. -27mm
LOOM -15mm



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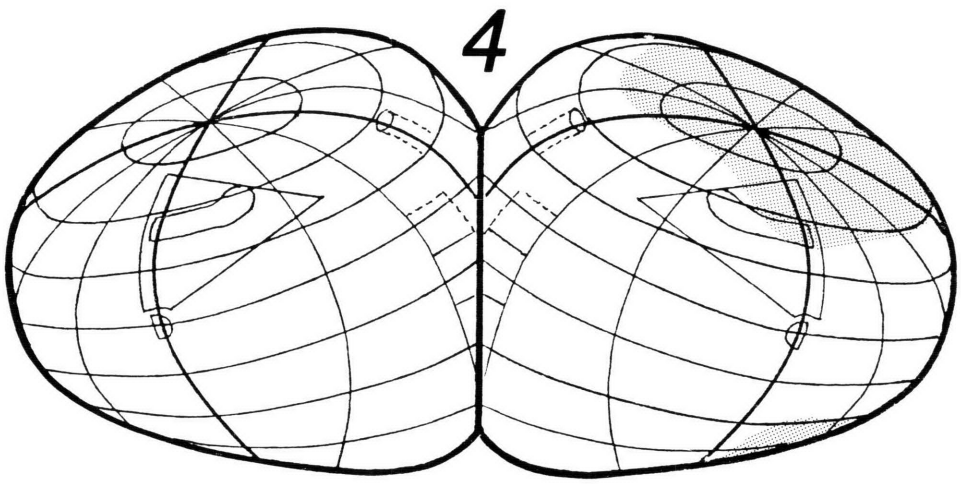
LOOM +6mm

Figure 7



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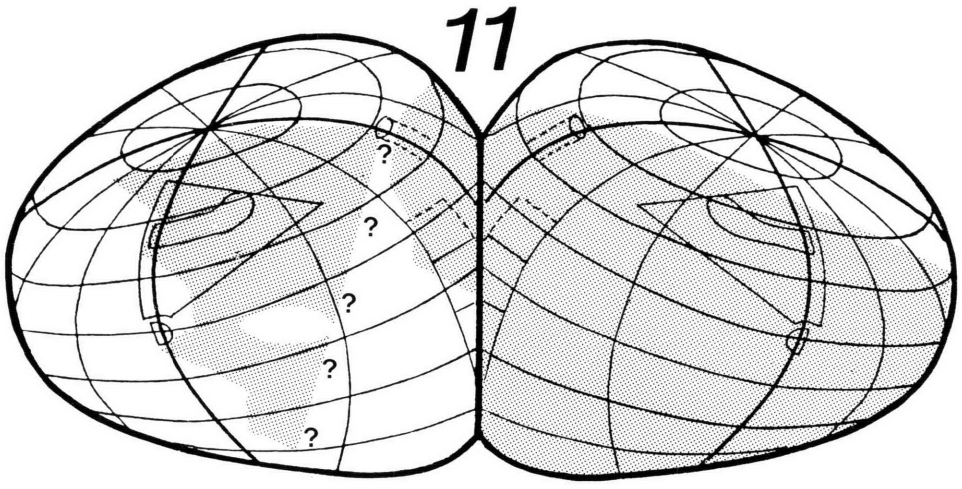

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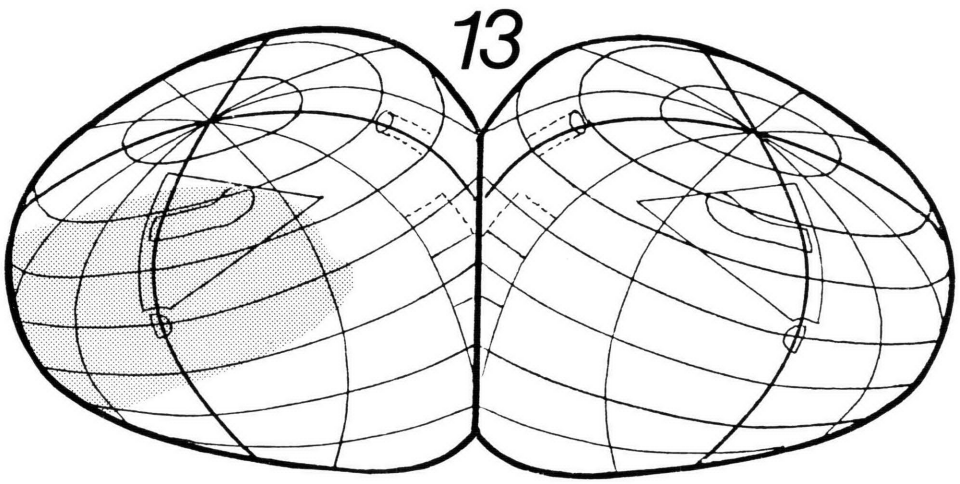
LOOM 0mm

Figure 8



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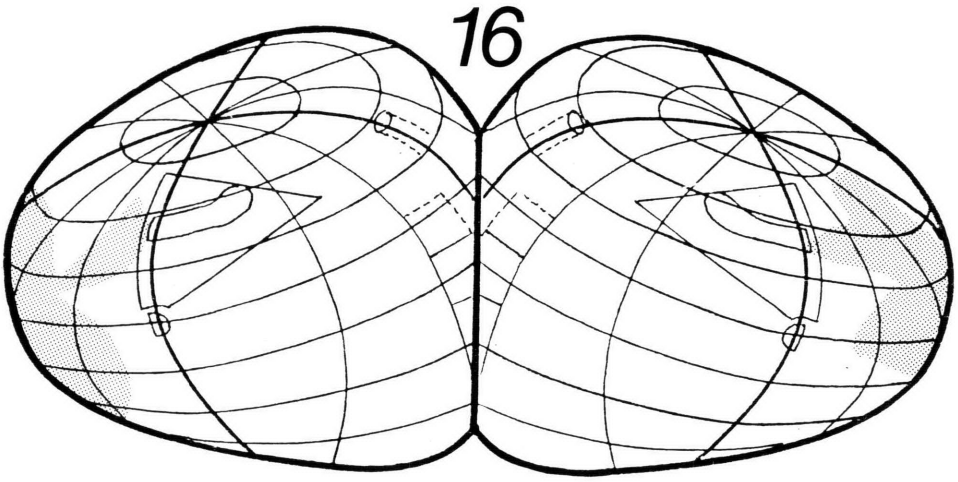

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LOOM +6mm

Figure 9

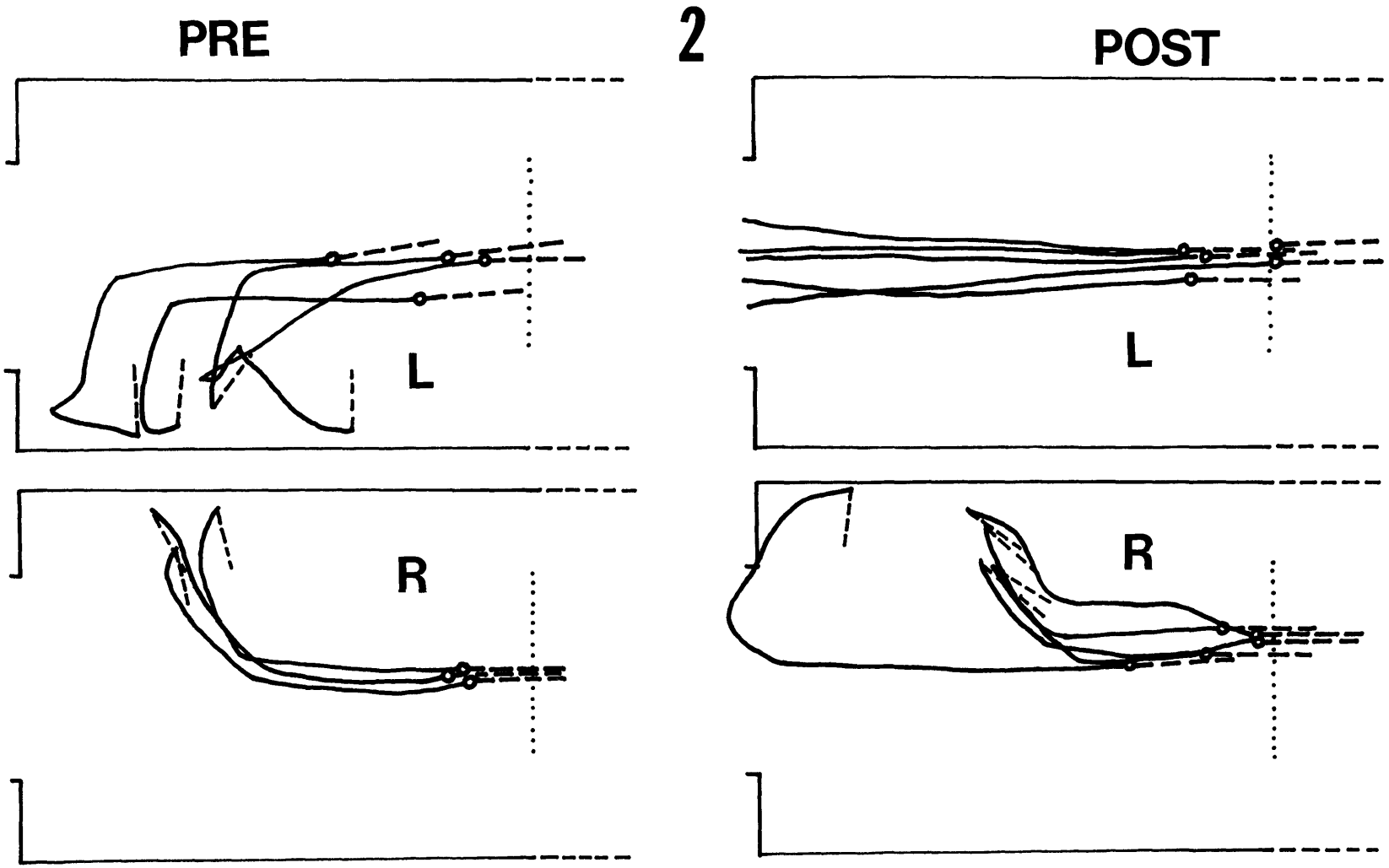

Figure 10

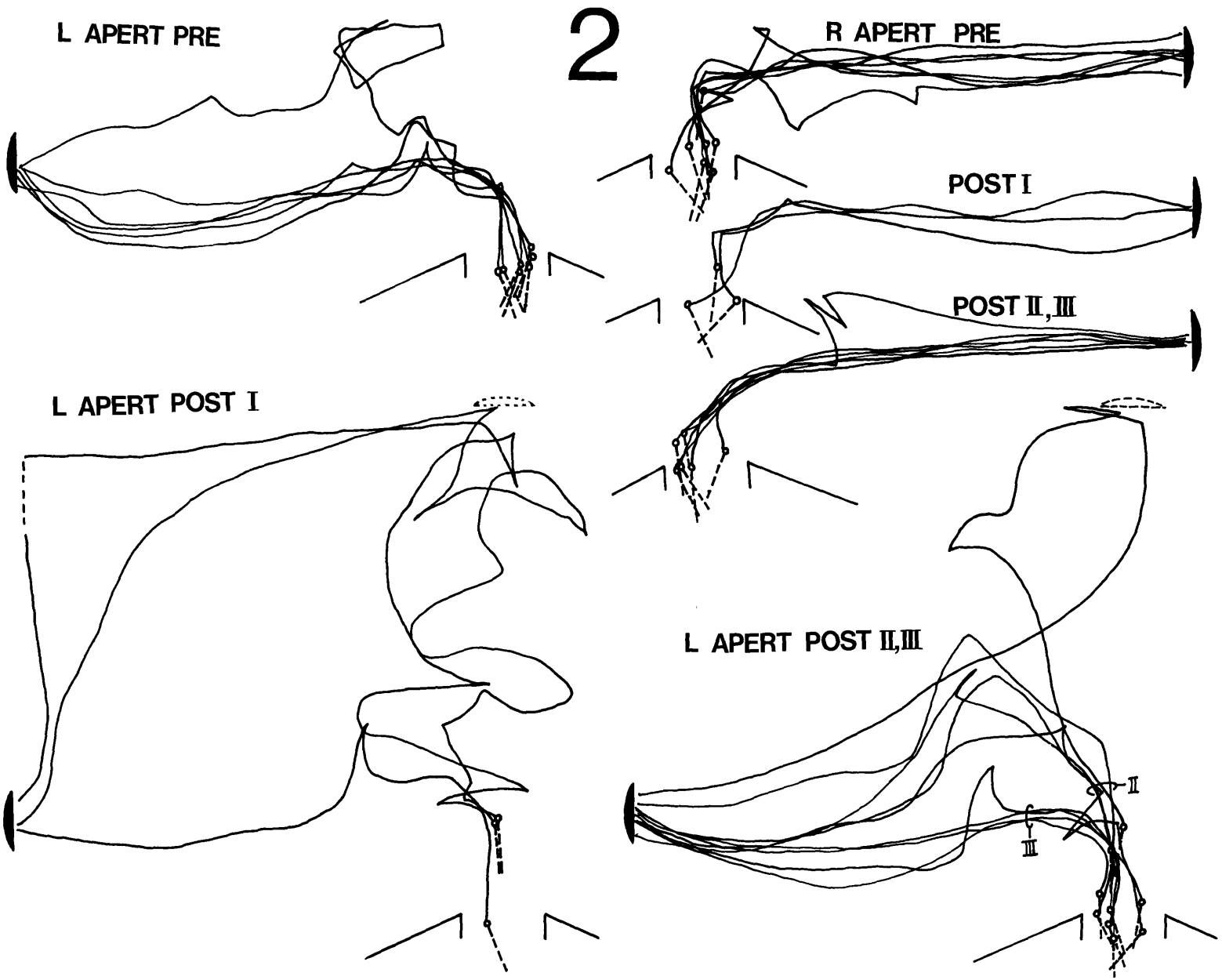
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Figure 11

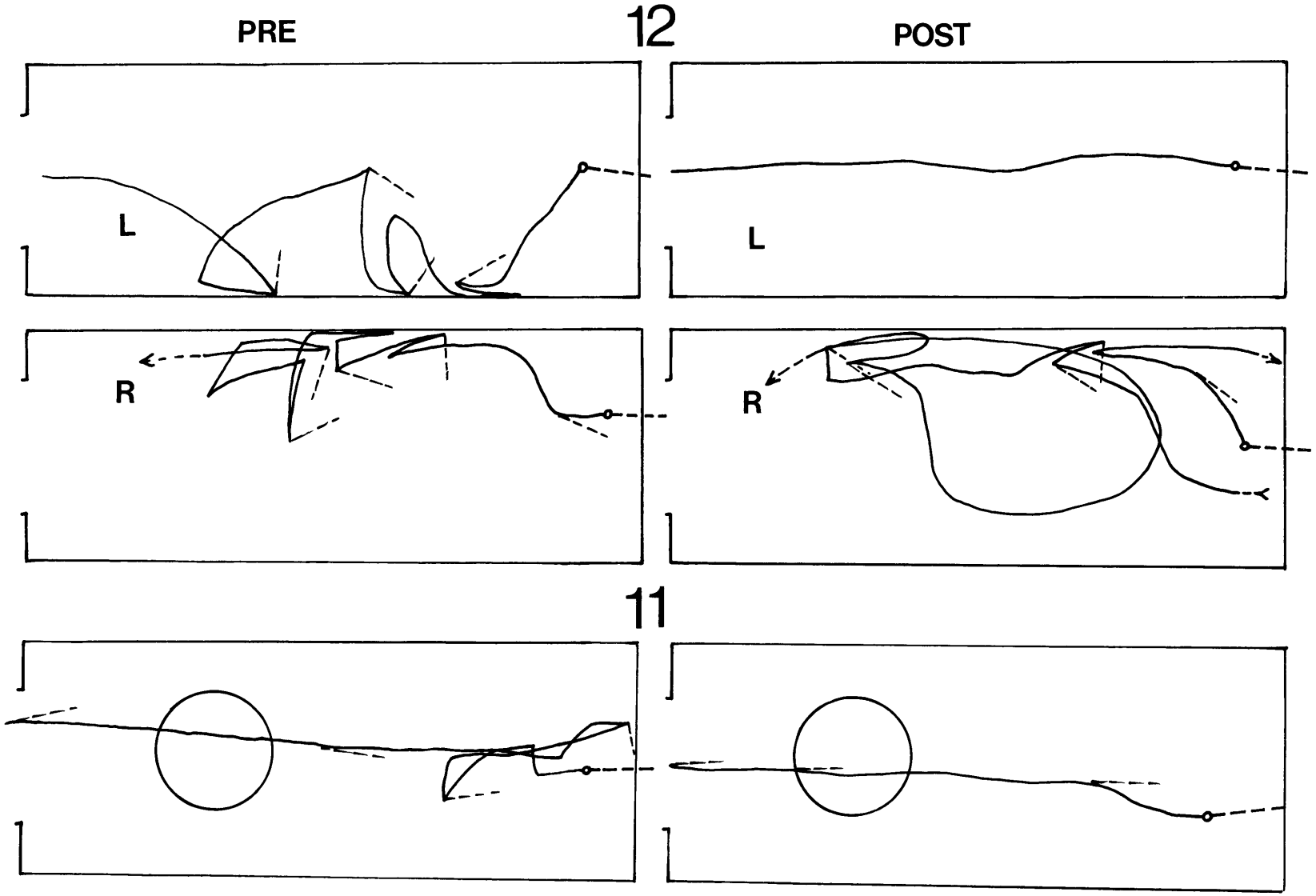
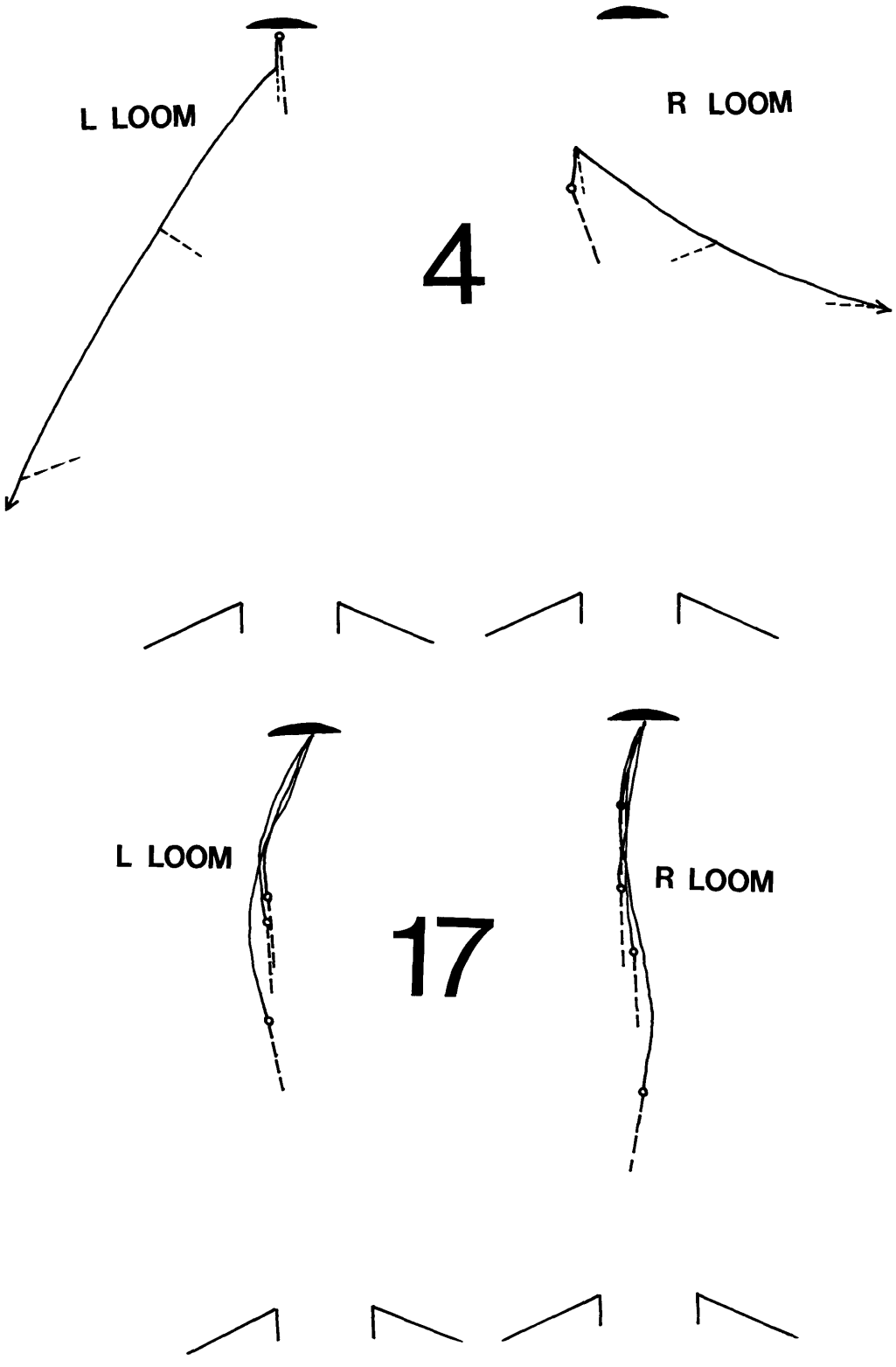


Figure 12



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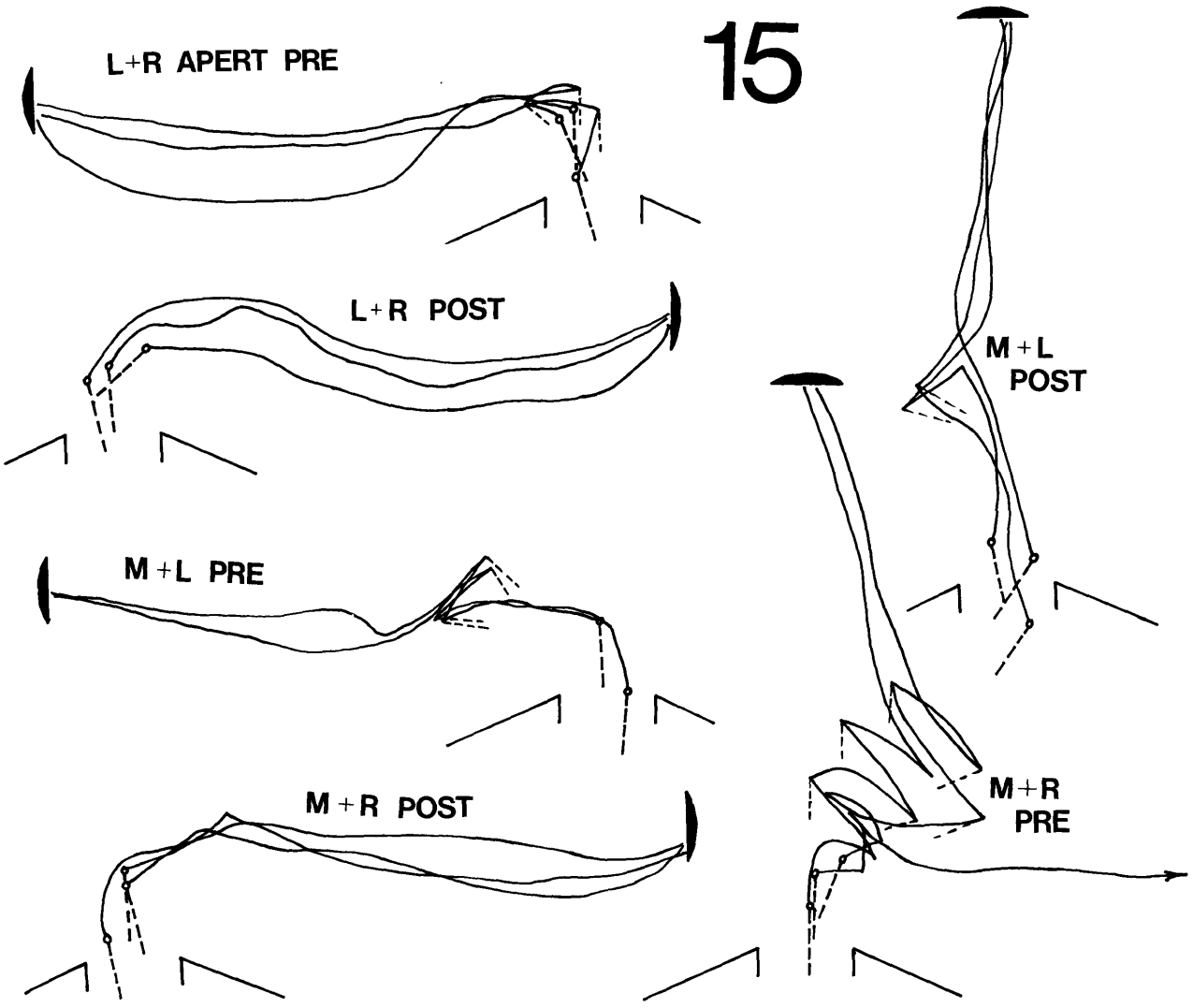

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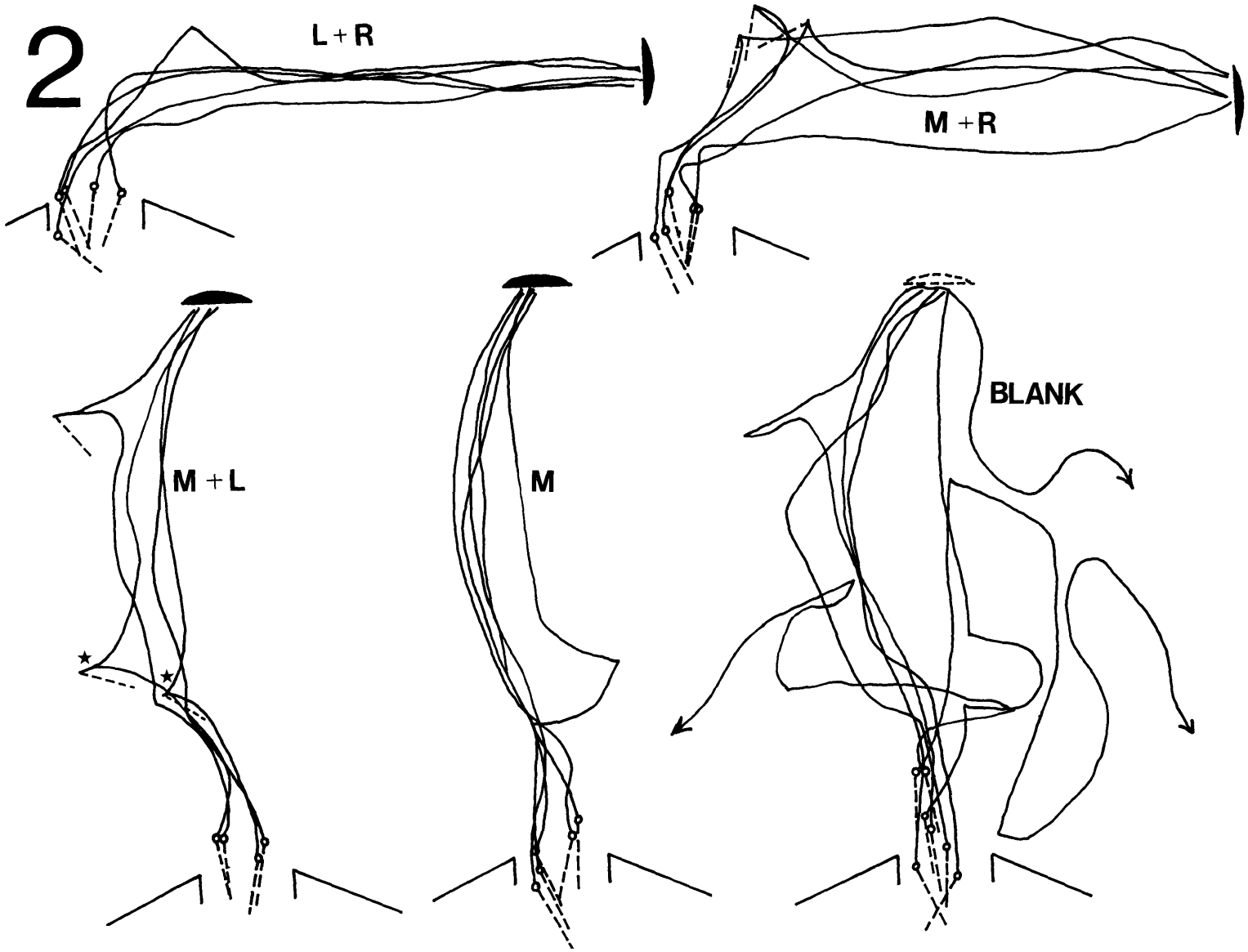

Figure 15

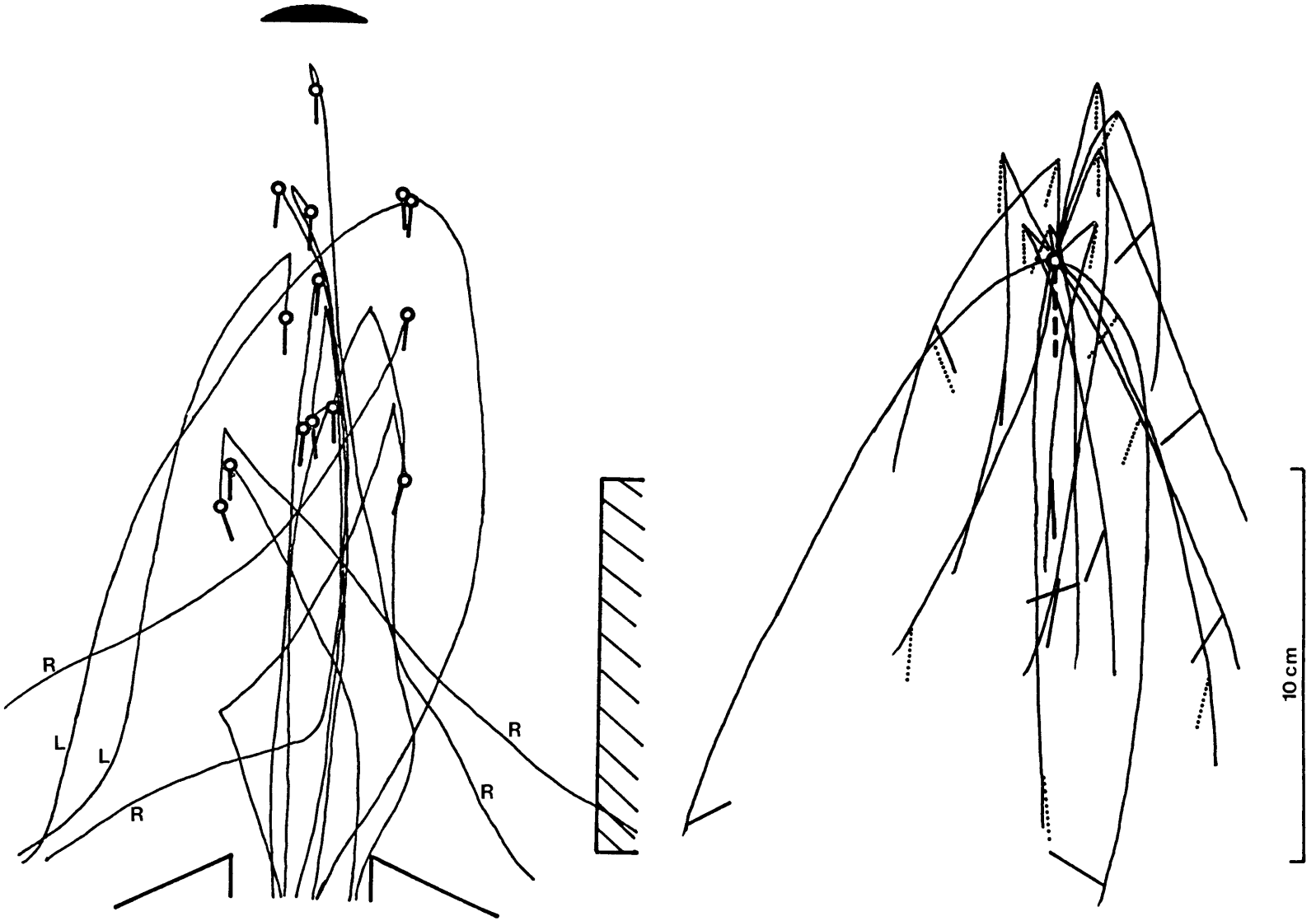

Figure 16

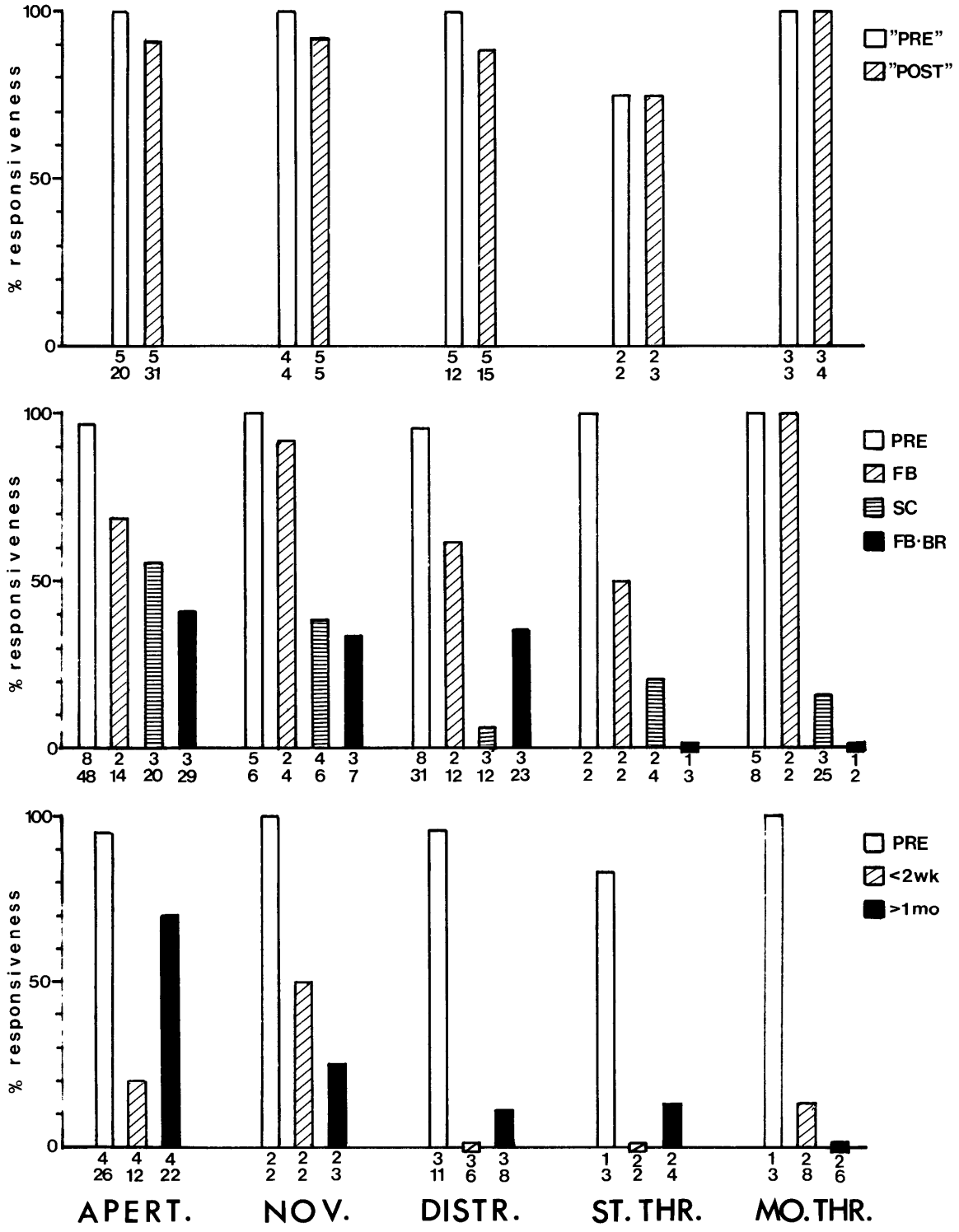
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Figure 17